







Libr. Off. copy

SMITHSONIAN

MISCELLANEOUS COLLECTIONS

VOL. 97



"EVERY MAN IS A VALUABLE MEMBER OF SOCIETY WHO, BY HIS OBSERVATIONS, RESEARCHES,
AND EXPERIMENTS, PROCURES KNOWLEDGE FOR MEN"—SMITHSON

(PUBLICATION 3529)

CITY OF WASHINGTON
PUBLISHED BY THE SMITHSONIAN INSTITUTION

1939

The Lord Baltimore Press
BALTIMORE, MD., U. S. A.

ADVERTISEMENT

The Smithsonian Miscellaneous Collections series contains, since the suspension in 1916 of the Smithsonian Contributions to Knowledge, all the publications of the Institution except the Annual Report, the annual pamphlet describing the Institution's field-work, and occasional publications of a special nature. As the name of the series implies, its scope is not limited, and the volumes thus far issued relate to nearly every branch of science. Papers in the fields of biology, geology, anthropology, and astrophysics have predominated.

C. G. ABBOT,

Secretary of the Smithsonian Institution.

CONTENTS

1. STRONG, WILLIAM DUNCAN; KIDDER, ALFRED, II; and PAUL, A. J. DREXEL, JR. Preliminary report on the Smithsonian Institution-Harvard University archeological expedition to northwestern Honduras, 1936. 129 pp., 16 pls., 32 figs., Jan. 17, 1938. (Publ. 3445.)
2. JOHNSTON, EARL S. Plant growth in relation to wave-length balance. 18 pp., 4 pls., Jan. 12, 1938. (Publ. 3446.)
3. RESSER, CHARLES ELMER. Middle Cambrian fossils from Pend Oreille Lake, Idaho. 12 pp., 1 pl., Jan. 3, 1938. (Publ. 3447.)
4. SCHMITT, JOHN B. The feeding mechanism of adult Lepidoptera. 28 pp., 12 figs., Jan. 10, 1938. (Publ. 3448.)
5. STIRLING, M. W. Three pictographic autobiographies of Sitting Bull. 57 pp., 46 pls., July 22, 1938. (Publ. 3482.)
6. SNODGRASS, R. E. Evolution of the Annelida, Onychophora, and Arthropoda. 159 pp., 54 figs., Aug. 23, 1938. (Publ. 3483.)
7. WEDEL, WALDO R. The direct-historical approach in Pawnee archeology. 21 pp., 6 pls., Oct. 19, 1938. (Publ. 3484.)
8. BUSHNELL, DAVID I., JR. Drawings by George Gibbs in the Far Northwest, 1849-1851. 28 pp., 18 pls., 4 figs., Dec. 30, 1938. (Publ. 3485.)
9. DEIGNAN, H. G. A new nuthatch from Yunnan. 2 pp., Oct. 10, 1938. (Publ. 3486.)
10. RESSER, CHARLES ELMER. Fourth contribution to nomenclature of Cambrian fossils. 43 pp., Dec. 17, 1938. (Publ. 3487.)
11. WEINTRAUB, ROBERT L. An assay method for growth-promoting substances utilizing straight growth of the *Avena* coleoptile. 10 pp., 1 pl., Dec. 31, 1938. (Publ. 3488.)
12. RESSER, CHARLES ELMER. The Spence shale and its fauna. 29 pp., 6 pls., Jan. 20, 1939. (Publ. 3490.)

SMITHSONIAN MISCELLANEOUS COLLECTIONS

VOLUME 97, NUMBER 1

PRELIMINARY REPORT ON THE
SMITHSONIAN INSTITUTION-HARVARD UNIVERSITY
ARCHEOLOGICAL EXPEDITION TO NORTHWESTERN
HONDURAS, 1936

(WITH 16 PLATES)

BY

WILLIAM DUNCAN STRONG

Anthropologist, Bureau of American Ethnology

ALFRED KIDDER II

Peabody Museum, Harvard University

AND

A. J. DREXEL PAUL, JR.

Peabody Museum, Harvard University



(PUBLICATION 3445)

CITY OF WASHINGTON
PUBLISHED BY THE SMITHSONIAN INSTITUTION
JANUARY 17, 1938



PROCESSIONAL FIGURES ON A YOJOA POLYCHROME VASE.
MAYOID TYPE, SITE 2, LA CEIBA
(From a painting by E. G. Cassedy.)

SMITHSONIAN MISCELLANEOUS COLLECTIONS

VOLUME 97, NUMBER 1

PRELIMINARY REPORT ON THE
SMITHSONIAN INSTITUTION-HARVARD UNIVERSITY
ARCHEOLOGICAL EXPEDITION TO NORTHWESTERN
HONDURAS, 1936

(WITH 16 PLATES)

BY

WILLIAM DUNCAN STRONG

Anthropologist, Bureau of American Ethnology

ALFRED KIDDER II

Peabody Museum, Harvard University

AND

A. J. DREXEL PAUL, JR.

Peabody Museum, Harvard University



(PUBLICATION 3445)

CITY OF WASHINGTON

PUBLISHED BY THE SMITHSONIAN INSTITUTION

JANUARY 17, 1938

The Lord Baltimore Press
BALTIMORE, MD., U. S. A.

CONTENTS

	PAGE
Introduction	I
Brief geographic setting.....	2
Ethnic and linguistic background.....	8
Early historic contacts in northwestern Honduras.....	19
Archeological explorations	27
Chamelecon River	27
Naco	27
Las Vegas	34
Tres Piedras	35
Other sites	37
Ulua and Comayagua Rivers.....	39
Las Flores Bolsa.....	39
Santa Rita (farm 17).....	45
Playa de los Muertos (farm 11).....	62
Other sites	76
North end of Lake Yojoa.....	76
Aguacate and Aguatal.....	80
La Ceiba	90
Site 1	91
Site 2	94
Site 3	99
Causeway and "canal" near Jaral.....	100
Pyramids and stone statues near Los Naranjos.....	102
Excavations on the northern border of Los Naranjos.....	105
The older horizon at Los Naranjos.....	111
Other sites	115
Summary and tentative conclusions.....	118
Literature cited	125
Explanation of plates.....	127

ILLUSTRATIONS

PLATES

	PAGE
1. (Frontispiece) Processional figures on a Yojoa Polychrome vase of Mayoid type, site 2, La Ceiba.....	title
2. Various Chamelecon and Ulua River sites.....	130
3. Naco sherds	“
4. Naco sherds and artifacts.....	“
5. Upper Ulua Polychrome pottery types, Las Flores.....	“
6. Upper Ulua Polychrome pottery types, Las Flores.....	“
7. Ulua Polychrome, Bold Geometric pottery types, Santa Rita and Naranjo Chino	“
8. Ulua Polychrome, Mayoid pottery types, Santa Rita.....	“
9. Ulua Bichrome sherds, from deepest level at Santa Rita.....	“
10. Playa de los Muertos Bichrome sherds.....	“
11. Playa de los Muertos Bichrome sherds and figurines.....	“
12. Yojoa Polychrome vessels, Mayoid types.....	“
13. Yojoa Polychrome vessels, Bold Animalistic and other types.....	“
14. Yojoa Polychrome vessels, Bold Animalistic and other types.....	“
15. Early ceramic types at Lake Yojoa.....	“
16. Los Naranjos, Lake Yojoa.....	“

TEXT FIGURES

	PAGE
1. Map of northwestern Honduras.....	4
2. Map of the region around Naco.....	7
3. Sketch map of the ruins of Naco.....	30
4. North wall of cross-section trench through mound 3, Naco.....	31
5. Map of the lower Ulua and Chamelecon Rivers.....	40
6. West wall of excavation 1, Santa Rita (farm 17).....	47
7. Hollow figurines, whistles, and “candelario”, from the Ulua Polychrome period, Santa Rita (farm 17).....	52
8. Ulua Polychrome, Bold Geometric tripod dish, excavation 2, Santa Rita (farm 17)	54
9. Unusual Ulua Polychrome, Bold Geometric dish, excavation 2, Santa Rita (farm 17).....	55
10. Ulua Polychrome, Bold Geometric bowl, excavation 2, Santa Rita (farm 17)	56
11. Ulua Polychrome bowl, excavation 2, Santa Rita (farm 17).....	57
12. Ulua Polychrome bowl, excavation 2, Santa Rita (farm 17).....	58
13. Ulua Polychrome, Mayoid vase, excavation 2, Santa Rita (farm 17)...	59
14. Inside design from Ulua Polychrome, Lower Mayoid vases (pl. 8, a, b), excavation 1, Santa Rita (farm 17).....	60
15. Ulua Polychrome Bowl, excavation 2, Santa Rita (farm 17).....	61
16. North wall of excavation 1, showing stratification, Playa de los Muertos (farm 11)	64

PAGE

17. Outlines of vessels of the Playa de los Muertos culture obtained by Dorothy H. Popenoe.....	70
18. Outlines of vessels of the Playa de los Muertos culture obtained by Dorothy H. Popenoe.....	71
19. Polychrome vase of Uluu Lower Mayoid type.....	77
20. Sketch map of archeological sites around the north end of Lake Yojoa..	78
21. Yojoa Polychrome bowl, Bold Animalistic type, Aguacate.....	82
22. Yojoa Polychrome pot, Bold Animalistic type, Aguatal.....	84
23. Yojoa Polychrome bowl, Bold Animalistic type, Aguacate.....	85
24. Yojoa Polychrome tripod dish, Bold Animalistic type, Aguacate.....	86
25. Yojoa Polychrome bowl, Bold Animalistic type, Aguacate.....	86
26. Outline of Yojoa Polychrome pot showing "vestigial" spout, Aguacate.	87
27. Yojoa Polychrome cooking pot, Aguatal.....	88
28. Yojoa Polychrome bowl, Mayoid type, Aguacate.....	89
29. Yojoa Polychrome bowl, Mayoid (?) type, Aguacate.....	90
30. Yojoa Polychrome vase, Mayoid type, Aguacate.....	91
31. Cross-section of west wall, site 1, Los Naranjos, showing house floor, burial, and superimposed cultural horizons.....	107
32. Cross-section of excavation A, near site 1, Los Naranjos, showing stratified cultural horizons.....	113

PRELIMINARY REPORT ON THE
SMITHSONIAN INSTITUTION-HARVARD UNIVERSITY
ARCHEOLOGICAL EXPEDITION TO NORTHWESTERN
HONDURAS, 1936

BY WILLIAM DUNCAN STRONG
Anthropologist, Bureau of American Ethnology;

ALFRED KIDDER, II
Peabody Museum, Harvard University;

AND

A. J. DREXEL PAUL, JR.
Peabody Museum, Harvard University

INTRODUCTION

The present paper presents in tentative and outline form certain major results of the Smithsonian Institution-Harvard University Archeological Expedition to northwestern Honduras in 1936. The expedition personnel included the senior author as leader and representative of the Bureau of American Ethnology, Smithsonian Institution, and the two other authors as representatives of the Peabody Museum of Harvard University. Mrs. Strong and Mrs. Kidder accompanied the expedition in the field and performed invaluable services in cataloging and caring for the collections. The purpose of the expedition was twofold: to extend the work carried on by the Smithsonian Institution in northeastern Honduras in 1933, and to follow up earlier work on the Ulua River so successfully inaugurated, under the auspices of the Peabody Museum, by George Byron Gordon and by Mrs. Dorothy Hughes Popenoe. The discoveries of Mrs. Popenoe at Playa de los Muertos in 1928 and 1929 opened new vistas in Honduras archeology, and her untimely death was a sad blow to science and to all who were fortunate enough to know her. In a sense our work was merely a continuation of that which she had so ably begun. The original suggestion for the present expedition came from Dr. Wilson Popenoe, and it was due to him that the successful cooperative effort was launched and completed.

The expedition received cordial support from the government of the Republic of Honduras, and our warmest thanks are extended to the

officials in Tegucigalpa and elsewhere who not only furthered the cause of science but put us deeply in their debt for many personal courtesies. Similarly, the officials of the United Fruit Company, both in the United States and in Honduras, furnished very material aid in ways too numerous to mention. Without this generous assistance our results would have been tremendously curtailed. Considerations of space prevent listing the many people who aided us in our work, but we cannot forbear mentioning Mr. Walter S. Turnbull, and Mr. Reginald Hamer. To them and to many other persons in Honduras we are deeply grateful. Later, in the final report, it will be possible to acknowledge more adequately our appreciation of the many courtesies, both official and personal, which we received on every hand.

Our choice of this particular area for excavation was based on numerous geographic, historic, ethnographic, and archeological considerations. For this reason we have devoted considerable space to these important factors. Viewed against this background, it is hoped that a condensed account of our excavations may have value. In due course a final report will be prepared by the senior author for publication by the Peabody Museum. As this may not appear for some time, it seems advisable to make our major results available without undue delay. Most of this important area still awaits adequate excavation, and it is our hope that these notes and sketch maps may be of value to future scientific explorers and excavators.

BRIEF GEOGRAPHIC SETTING

The general area covered by this report includes the eastern portion of the Department of Cortes, the western border of the Department of Yoro, and certain places on the eastern border of the Department of Santa Barbara, all within the Republic of Honduras.¹

From the archeological standpoint, however, modern political boundaries are of minor importance compared to factors of terrain and drainage, which conditioned aboriginal human occupation no less than they do that of the present inhabitants. Of primary importance

¹ See map, fig. 1. The best general maps of Honduras at present are the "Carta General de la Republica de Honduras, America Central, of the Pan-American Institute of Geography and History, 1933", and the "Mapa General de la Republica de Honduras, Levantado por el Prof. Jesus Aguilar Paz, 1933." These maps are far superior to any of their predecessors. Many contradictions still exist, however, owing to the present inadequacy of cartographic exploration in much of Honduras. The present map (fig. 1) is primarily based on that of Dr. Paz.

is the fact that at this point occurs one of the easiest passages across the Central American Isthmus from Tehautepec to Panama.²

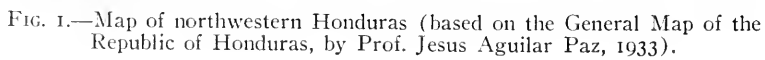
From the mouth of the Ulua River, where it enters the Gulf of Honduras, a series of elevated valleys extend up the Rio Blanco to Lake Yojoa, over the plateau of Siguatepeque, across the Plains of Comayagua, and down the valley of the Goascaran River into the Gulf of Fonseca and the Pacific. It can hardly be coincidental that it is at this point that the higher aboriginal cultures of the Pacific Highland extend north to the Caribbean Sea, in marked contrast to the lower cultures of the remainder of the Atlantic Lowland region in Honduras. The present archeological reconnaissance covers the northern half of this natural transition area between the Pacific Highland and the Atlantic Lowland regions.

If we include the valley of the Chamelecon River, which at no very distant time emptied into the Gulf of Honduras through the Ulua River, this entire area from Lake Yojoa north may be termed the Ulua drainage. The lower portions of the Ulua and Chamelecon Rivers flow through the Plain of Sula, a rich alluvial valley, down to their respective mouths in the great mangrove swamps extending along the Gulf of Honduras from Puerto Cortez almost to Tela. Because of these swamps and their shallow, silted-up channels, neither river offers much inducement to modern navigation, whereas such impediments were probably of small import to the numerous trading canoes of pre-Conquest times. Above the mangrove swamps, which extend some 20 kilometers upstream, is the rich valley floor that today is covered with banana plantations. Formerly the valley supported a rich tropical flora, described by Gordon (1898) and others, but at present, except for isolated remnants in swamps and low areas, the great mahogany, ceiba, and other trees, have been replaced by the ubiquitous banana. To the northwest the Ulua valley is hemmed in by the great Mountains of Omoa, which reach a height of 7,000 to 8,000 feet. To the east occur the Mountains of Mico Quemado and Tiburon. Between these two ranges the Ulua-Chamelecon valley reaches a breadth of some 45 kilometers, terminating about 75 kilometers in a direct southwest line from the mouth of the Ulua at Potrerillos, where the

² This has been pointed out time and again in the voluminous literature referring to the much-talked-of but never completed transoceanic railroad across Honduras.

See Squier, 1858 and 1870, and Wells, 1857. Although perhaps unduly optimistic on some points, Squier's various reports remain the best general geographic descriptions of Honduras.

Wells gives a detailed and delightful picture of Honduran life in the middle of the last century. So far as the remote interior is concerned, much of his description holds good today.



bordering mountains converge and the Ulua splits up into its three main branches (maps, figs. 1, 5). These are, from north to south, the Comayagua, the Rio Blanco, and the Ulua proper. The Chamelecon, after running parallel to the Ulua for some 50 kilometers above its mouth, turns north into mountains, where, as a rapid mountain stream, it extends almost as far southwest as Copan. Similarly, the three branches which form the Ulua are rapid, clear streams, in marked contrast to the slow moving, muddy lower Ulua and Chamelecon.

Owing to its configuration and the mountainous character of its terrain, Honduras has a wide variety of climates and seasons. In general, however, the dry season in the region we are considering begins in December or January and extends until June or early July. The temperature, which is pleasantly low in the early part of the dry season, increases as the wet season approaches. The rainy season is cooler, but more unpleasant, owing to rain, wind, and great humidity. Moisture brought by the northeast trade winds is deposited when they hit the high mountains bordering the Ulua valley. Thus, despite their relatively short courses, the Ulua-Chamelecon tributaries at times carry a tremendous volume of water. These rivers rise to their greatest heights about October and flood the valleys. A smaller rise occurs in the late Spring. As the rivers spread over the lower valleys, they deposit the sediment brought down from the mountains, and in this way the valley has been aggraded or built up. As proved by human occupation levels buried *in situ* 6 meters or more deep along the present channels, this building-up process has been relatively rapid and continuous.³

As the present rivers shift their channels across the valley floor, they thus expose in their steep banks the various human occupation strata of past centuries, which elsewhere in the valley are inaccessible, because of depth and lack of surface indication. The majority of the sites investigated along the Ulua by the present expedition were of this type.

Whereas the lower Ulua valley was formerly covered with a luxuriant rain forest, the sites which we worked on the upper Chamelecon

³ Yde, 1936, p. 39, in our opinion, exaggerates the difficulties due to depth of deposit facing the archeologist in this region. Nevertheless, there is no doubt that the earliest human remains in the lower Ulua valley may be buried at inaccessible depths. However, as the present report demonstrates, it is possible to obtain stratification. Gordon, 1898, shows the manner in which the rivers cut and shift their channels as well as the dangers of re-deposition which must be borne in mind by the archeologist. Neither Mrs. Popenoe nor the present writers encountered cultural remains at the extreme depths mentioned by Gordon and Yde.

in the vicinity of Naco (map, fig. 2) are located on clear, rapid streams. These streams are bordered by narrow strips of tropical forest, but back from these are steep hills or elevated rocky plains covered with pines and oaks. There is no reason to believe that the environment here was different in aboriginal times. It is a region admirably adapted to maize. Abundant food supplies possessed by the numerous Indian pueblos, as well as the occurrence of gold in the surrounding mountains, early attracted the Spaniards to these mountain valleys. The climate appears to be much more healthful than that of the lower river valleys.

The northern end of Lake Yojoa, where other excavations were carried on, offers a similar environment. This marks our most southerly working point as well as the limit of the Uluá drainage in this direction, since Lake Yojoa in part drains through an underground channel into the Rio Blanco. To the south, it is said to drain into the Santa Barbara River by means of the Jaitique River and by subterranean channels, principally the Rio Sacapa and the Rio Salala.⁴ We did not investigate the southern end of the lake.

Lake Yojoa is located in a small mountain valley or *bolson* at an altitude of some 2,050 feet. The auto road from the north coast to Tegucigalpa utilizes the lake as a water connection by means of automobile ferries. To reach Jaral, the little town on the north shore, one leaves the low banana country at Potrerillos and climbs through rocky hills covered with oak, pine, and scrub, following the Rio Blanco River, which is crossed only once at the little town of that name. Just before the road reaches the lake, the grade increases sharply and then drops down onto the small triangular plain bordering the lake (map, fig. 20). This bush-covered plain is bounded on the east by low pine-covered hills, and on the north by high (5,000-6,000 feet) volcanic mountains. We suspect that this plain originally supported a heavy rain forest, but both the aboriginal and modern inhabitants have long practised milpa-type farming here, and today there exist few remnants of the original forest. With the exception of open, rolling, pine-covered hills on the northeast shore near Agua Azul, the remainder of the lake is bordered by steep slopes covered with rain forest. At the southern extremity of the lake, there is a considerable belt of low, swampy land, most of which is overflowed when the lake is full. Beyond the water-

⁴ Published reports and maps of Lake Yojoa are utterly inadequate. Squier, 1858, pp. 96-104, and 1860, pp. 58-63, is still the authority. The lake has been studied from time to time by Honduran and American engineers, but we know of no up-to-date maps or reports. Amory Edwards, and Squier, 1860, describe 10 outlets.

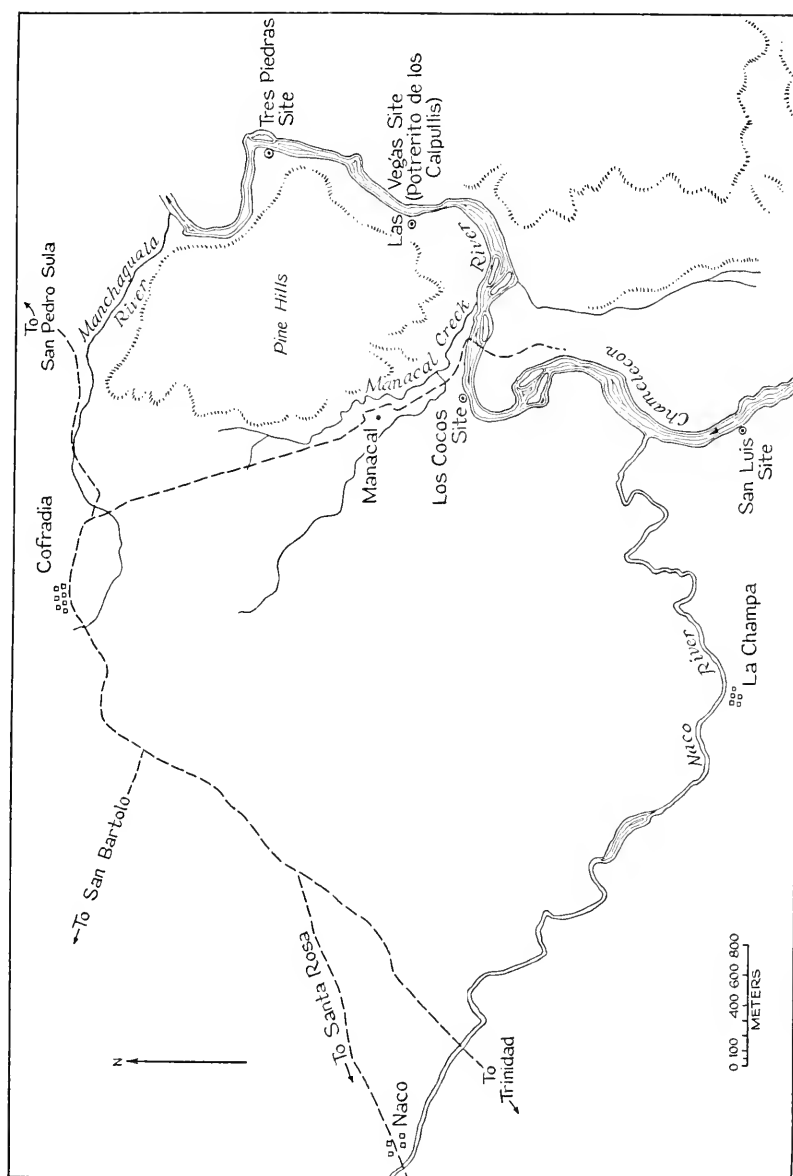


FIG. 2.—Map of the region around Naco (based on a map of the Compañía Agrícola De Ulua, 1935).

shed to the south in the vicinity of Taulebé and San José, there are fertile plains and valleys. These are separated from the Comayagua valley by the high plateau of Siguatepeque.

In general, therefore, it can be said that the sites investigated by us in the Ulua drainage occupy two main environmental regions: First, those on the lower Comayagua and Ulua Rivers, located in the rain forests of the broad, alluvial river valleys, and second, mountain valleys, as at Naco and at Lake Yojoa, where the elevation was considerably greater, the rain forest limited to the borders of stream or lake, and the more open pine and oak association close at hand.

ETHNIC AND LINGUISTIC BACKGROUND

At the present time there are no obvious, aboriginal remnants of population in the part of Honduras considered in this report. It is true that the present population of the region is in considerable part made up of assimilated Indian groups, but the language is Spanish and the culture Latin American. Isolated groups of Jicaque Indians are reported as still living in the more remote parts of the Department of Yoro.⁵

It is possible that Lenca-speaking Indians may still be found in our region, and groups of Chorti Maya occur in the departments to the south and west, but, as yet, ethnographic and linguistic research in Honduras has received little attention. If we desire to connect the archeological remains with historic Indian groups, it is therefore necessary to turn back the pages of history and consider the region at the time of the Spanish Conquest.

Early sources on northwestern Honduras are fairly numerous, including Cortez, Bernal Diaz, Palacio, Las Casas, Torquemada, Marroquin, Montejo, Palaez, Pedraza, Espino, and the historians Herrera, Oviedo, and Gomara, but, with the exception of the first three, the grains of ethnography to be gleaned from the works of these writers seem rather scant. In a later paper other sources will be considered, but for the present we shall confine ourselves to the most important primary sources and more recent general studies.

As was the case in regard to the geography of Honduras, one must still consult E. G. Squier's "States of Central America", 1858, regarding the ethnography of Honduras. Similarly, H. H. Bancroft's

⁵ Described by Habel, 1886, p. 17. In June 1933 the senior author was told by Mr. Acley, then American Consul at Tegucigalpa, of a very primitive group of Jicaque Indians he had visited that year near the town of Morale, in the Sierra de la Flor of the Department of Yoro, near the Olancho line. From photographs, they appeared very similar to those described by Habel.

"Native Races" (1882) is a treasure house of ethnographic source material, and the same author's "History of Central America" (1883) not only indicates the sources but also the major trends of native and European contact in the period of conquest. More recently Cyrus Thomas and John R. Swanton (1911) have presented in brief form the salient facts regarding the distribution of Indian languages in Honduras as part of their study of the languages of Mexico and Central America. Preeminent in this field, however, is the voluminous and detailed work of Walter Lehmann, who in a preliminary report in 1910, and in "Zentral Amerika" (1920), has given us a wealth of data based on close examination of the sources as well as personal linguistic work in the field. In addition to an intensive study of original sources and present-day Indian dialects, Lehmann has also included many sweeping theoretical generalizations. The latter, however, concern us less in the present study than do the specific references to linguistic and cultural distributions in Honduras at the time of the Conquest.

In general, the linguistic maps of Thomas and Swanton (1910), and Lehmann (1920) agree as regards the distribution of native languages in the Ulua drainage. Both place Chol, Chorti, and other Maya-speaking groups to the west of the Ulua River proper. Following Lehmann, we find that the Lenca occupied a large area around Lake Yojoa, extending north almost to the junction of the Comayagua and the Ulua. From here to the coast the valley of the Ulua and Chamelecon Rivers was Jicaque territory. To the west, Lenca and Jicaque territory bordered on that of the Chorti and Chol Maya, Copan being one center of Chorti occupation. The Lenca and Jicaque demesnes extended east to that of the Paya who with the Sumu, occupied the northeastern corner of Honduras.⁶

To the south, peoples of Lenca speech extended to the Pacific coast. To the west they were bordered by the Pipil of Salvador along the Lempa River, and to the east by various Chiapanecan and Matagalpan groups (see linguistic maps, Thomas and Swanton, 1911, and Lehmann, 1920).

Thus it appears that all of the territory investigated by the present expedition was occupied by Jicaque and Lenca-speaking peoples at the time of the Conquest—with one very important exception. This was the occurrence in the same region of various Nahuatl-speaking pueblos along what appear to have been trade routes extending from southern Mexico and from the Pipil (Nahuatl) territory in Salvador. Leh-

⁶Linguistic and tribal distributions in Honduras have already been discussed in some detail; see Strong, 1935, pp. 7-19 and 140-172.

mann indicates one such line of late Nahuatl influence and settlement which crossed the Chamelecon River in the vicinity of Naco and extended east to the Nahuatl pueblos mentioned by Cortez, located a short distance south of Trujillo (Lehmann, 1920, vol. 2, p. 629 and map). Both Cortez and Bernal Diaz in their accounts of the traverse from Mexico to Honduras indicate the importance and vogue of these trade routes and mention the many pueblos engaged in trade which they visited (Bernal Diaz, 1916). Recent Nahuatl settlements would be thus expectable in the upper Chamelecon valley near Naco and probably elsewhere in the Ulua valley proper. These Nahuatl influences from southern Mexico were apparently quite recent, but the Pipil occupation of Salvador was much older. This is clearly indicated by Palacio (1860, pp. 21, 31, and 65), who points out the acquisition of the Pipil tongue by many neighboring groups originally of different linguistic affiliation. Moreover, Pipil cultural influences were obviously very active in southwestern Honduras at the time of which Palacio writes (i. e., 1576).

The name of the Ulua River was apparently derived from the Ulba language, which Palacio ascribes to Honduras (1860, p. 21). Both Squier (Palacio, 1860, p. 114) and Lehmann (1910, p. 747; 1920, vol. 2, p. 624) concur in this identification. The extension of the term Ulba, Ulua, or Ulvan to the Sumu is explained by Lehmann on the grounds that the Sumu, Jicaque and Matagalpan languages (including the Cacaopera and Lislique) are all basically related. This seems quite probable but has not yet been satisfactorily demonstrated. Since the Jicaque lived along the Ulua river, it is most probable that Palacio referred to them as the Ulba. Both Squier (Palacio, 1860, p. 114) and Lehmann (1920, p. 624) regard Palacio's designation "Chontal" as a general term for non-Pipil-speaking peoples. According to Lehmann, the term would include the Lenca with the Jicaque. Specifically, Palacio seems to refer to the Lenca when he speaks of the Taulepa. This is the old name for Lake Yojoa (Taulebé, according to Squier, 1860). In the Lenca language, Taulepa means "House of the Jaguars" (Lehmann, 1910, p. 747; 1920, vol. 2, p. 624). The jaguar was of special importance in Lenca mythology. Lehmann is convinced that the region around Lake Yojoa and the entire central portion of Honduras was occupied by the Lenca (the Taulepa of Palacio), and that the valley of the lower Ulua and the adjacent Department of Yoro was primarily occupied by Jicaque groups (the Ulba of Palacio). During the seventeenth century, the names Lenca and Jicaque were often confused, but, as indicated by the work of Thomas and Swanton, the general regions assigned to these groups by Lehmann seem accurate.

It is therefore apparent that our archeological investigations were made in a contact area between advanced Mayan and Nahuatl peoples to the west, and Lenca, Jicaque, and other less advanced groups to the east. As Lehmann points out (1920, vol. 2, p. 625, and map), Maya influence, as indicated primarily by archeological objects, extended well into Lenca territory, including all the region west of a line drawn from the junction of the Ulua and Comayagua Rivers southeast to the Gulf of Fonseca. Similar influences were also present in the lower Ulua valley and in Salvador. Moreover, Palacio (1860) clearly indicates that cultural influences from the Nahuatl Pipil of Salvador extended east well into Lenca territory during early historic times. Whether Lehmann's assumption that the language of the Lenca is related, on the one hand, with the Jicaque and the Paya, and on the other, with the Cacaopera, Matagalpa, Sumu, Ulua, Miskito, Rama-Guatuso, etc. (1920, vol. 2, p. 637), be accepted or not, there is little doubt that the majority of these languages are affiliated with major linguistic stocks to the south. There is at least a strong probability that the majority of these languages are in some degree related to the Chibchan linguistic stock centering in northern South America. As has been pointed out elsewhere (Strong, 1935, pp. 170-172), the scant ethnological information on certain of these groups likewise points to a southern derivation. On the other hand, Chol and Chorti Maya and Nahautl (Pipil and Aztecán) linguistic connections are clearly with the north. Thus the Ulua-Yojoa region comprised an important buffer area between two sets of cultural traditions and linguistic stocks, the one derived from Mexico and northern Central America, the other from southern Central America and, eventually, from South America. A very complex archeological situation is therefore expectable. It is, however, a situation that, when clearly understood, is certain to throw much new light on the ultimate derivation and development of the higher civilizations of the New World.

Since the historic occupants of our particular region were the Lenca and Jicaque Indians, we are particularly concerned with whatever ethnological information has survived concerning their cultural status at the time of the Conquest. Regarding the Jicaque, little is on record but for the Lenca, or at least their near neighbors and cultural kin, we have the brief but excellent account of Palacio. Speaking of the plain of Jiboa in the province of San Miguel, Salvador, he says that here the Indians begin to speak a new language, called the Chontal. He states that they "are a very rude people, but had anciently a great reputation for valor among their neighbors." His description of the customs observed prior to 1576 at Mictla, (Mita),

apparently a cultural center representing a blending of Pipil and Lenca ceremonies and customs, is so important that we quote it in full, following Squier's translation (Palacio, 1860, pp. 65-89).

Three leagues distant, is the village of Mictla, which anciently the Pipil Indians of this district held in great veneration; it was here they came to make their offerings and sacrifices, as did also the Chontals, and other neighboring Indians of different languages. Their modes of sacrificing differed in some respects from those of other parts. They had cues or temples, and teupas or priests of high authority, of which there are still many signs and traces.

Besides their cazique or secular lord, they had a kind of pope, called Tecti, who dressed in a long blue robe, and wore on his head a diadem, or sometimes a mitre embroidered with many colors, at the crown of which rose a cluster of very beautiful feathers, taken from a bird, called in this country, Quetzal. This pontiff carried in his hand a staff, which resembled the crook of a bishop, and he was obeyed in all spiritual things. After him, next in sacerdotal authority, was the tehu a matlini, who was the ablest diviner and the man best versed in their ancient books and in their arts. He it was who made auguries and foretold future events. After him were four priests called teupixquis, who went dressed in long robes, falling to their feet, each of different color, black, red, green and yellow. These were the counsellors of the pontiff, and directed all the superstitious ceremonies and follies of their religion. Their was also a kind of mayor-domo, who had charge of the sacred jewels and the instruments of sacrifice. He also opened the breasts of the victims of sacrifice, and tore out their hearts, and performed such other personal services as were requisite. Besides all these there were other functionaries, who played on the drums, trumpets and other instruments used in convoking the people to the sacrifices.

ELECTION OF THE POPE AND PRIESTS

When the chief priest died, he was buried in his own house, seated in a painted chair, and all the people mourned for him for fifteen days, with loud cries and lamentations. They also fasted during this period; but when this was over, the cazique and the wife, man or diviner selected a new pontiff by lot. It was requisite that he should be one of the four priests above mentioned. When the choice was made, they had great feasts and dances, and he who was chosen drew blood from his tongue and private parts, and offered it in sacrifice to the idols. He also named his successor in the priesthood, who was required to be a son of the deceased pontiff, if he had left one, if not, the son of some other priest. He filled also the other offices which at any time became vacant in the teupas, or temples. They adored the rising sun, and had two idols, one representing a man, whom they called Quetzalcoatli, and the other a woman named Itzqueye. All their sacrifices were made to them, and they had a calendar, with days specially set apart for each one, and on these the sacrifices were made.

SACRIFICES

Each year they had two principal and very solemn sacrifices; one at the commencement of summer, and the other at the beginning of winter. These were made in the interior of the sacred place or temple, and were of boys between the ages of six and twelve years, bastards, born among themselves.

MODE OF THESE SACRIFICES

They sounded their trumpets and drums for one day and night before the sacrifice, and when the people were assembled, the four priests came out from the temple, with four small braziers in which they burnt copal and caoutchouc; and the four together, turning in the direction of the rising sun, bent their knees to it, offering incense, and reciting words of invocation. After this they separated, and did the same in the direction of the four cardinal points, south, east, north and west, preaching and explaining their rites and ceremonies. When the sermon was finished, they retired within four houses or chapels which were built at the four corners of the temple, and there rested for a little while. They next went to the house of the high priest, which was close to the temple, and took thence the boy who was to be sacrificed, and conducted him four times around the court of the temple, dancing and singing. When the ceremony was finished, the high priest came out of his house, with the second priest and mayordomo, and ascended the steps of the temple, accompanied by the cazique and principal Indians, who, however, stopped at the door of the sanctuary. The four priests next seized the victim by his extremities, and the mayordomo coming out, with little bells on his wrists and ankles, opened the left breast of the boy, tore out his heart and handed it to the high priest, who put it into a little embroidered purse, which he closed. The priests received the blood of the victim in four jicaras, which are vessels made from the shell of a certain kind of fruit (the calabash), and, descending one after another into the court, sprinkled it, with their right hands, in the direction of the cardinal points. If any blood remained over, they returned it to the high priest, who put it back, with the purse containing the heart, into the body of the victim, which was interred in the temple itself. This was the kind of sacrifice made at the opening of the two seasons of the year.

The high priest, his second, and the four priests were accustomed to meet to ascertain, by sorcery and enchantment, if they should make war, or if their foes were coming to attack them; and if it appeared that such an event was to take place, they called together the cazique and war chief, and advised them of the approach of their enemies, and whether they should go to meet them. The cazique then assembled the soldiers, and all went out to battle. If he was victorious, he despatched a messenger to the high priest, advising him of the date of the occurrence, and on this information the diviner ascertained to which of the gods sacrifice was to be made. If to Quetzalcoatl, the ceremonies lasted fifteen days; if to Itzqueye, five days, and on each day they sacrificed a prisoner. These sacrifices were made as follows: All those who had taken part in the war, returned home in order, singing and dancing, and bringing with them those who were to be sacrificed, decorated with feathers and chalchuiques on their wrists and ankles, and with strings of cacao beans around their necks, the captains themselves conducting them in their midst. The pontiff and priests, at the head of the people, went out to meet the victors, with music and dancing; and when they encountered them, the captains delivered over the victims to be sacrificed, to the high priest; after which all went together to the court of their teupa, where they kept up the dancing night and day, for the periods above named. In the middle of this court was placed a block or bench of stone, on which the victim was stretched, the four priests holding him by the feet and hands. The sacrificer then came forward, loaded with plumes and bells, with a knife of flint, with

which he opened the breast of the victim, and took out his heart, and tossed it in the air in the direction of the four cardinal points, and finally threw it aloft directly in the middle of the court, in this way soliciting the divinity to accept the sacrifice, in return for the victory. This sacrifice was public to all the Indians, great and small.

During this period, the soldiers returning from the war, could not cohabit with their wives, but were obliged to sleep in certain calpules or barracks, which were given up to them for the occasion, by the young men who were learning the art of war. During the day they went to the houses of their women to eat and drink, and from thence to their plantations, always however, leaving a company to guard the town. The men sacrificed blood drawn from their private parts, and he who had most wounds in these was reputed to be most valiant. The women sacrificed blood drawn from their tongues and ears, and they sacrificed their entire bodies, taking up the blood with cotton and offering it to their idols—the men to Quetzalcoatl, and the women to Itzqueye.

Their superstitious ceremonies, at the time of planting their fields, were as follows: They put in little cups of calabash the seeds which they had selected for the purpose, and placed them before the altar of their idols. They next dug a trench in the ground, in which they planted the seeds regularly, covering them with earth; and over all they placed a large brazier, full of burning coals, on which they sprinkled copal and caoutchouc. The four priests then drew blood from their ears and nose, receiving it in certain large reeds, which they burnt before their idols. At other times they drew blood from their tongues and private members, and petitioned their gods to prosper the fruits of the earth, and give them abundant harvests. The high priest, in sacrificing, drew blood from the same parts, and with it anointed the feet and hands of the idols, invoking the demon, who spoke with him, and told him what kind of weather would follow, all of which was communicated to the people by the four priests, who always concluded by ordering the men to have connection with their wives, and then proceed to plant their fields. And such was the sacrifice of planting.

We come now to their sacrifices for hunting and fishing. They took a living deer to the courtyard of the cue or temple which they had outside of the town, where they strangled and skinned him, collecting all his blood in a vase, and cutting in small pieces the liver, lungs and stomach. These were put aside, with the heart, head and feet. They next cut up and cooked the deer by itself, and the blood by itself, and while these were cooking they had their dances. Next the high priest and his assistant took the head by the ears, and each of the four priests one of the feet, and the mayordomo put the heart in a brazier and burned it, with copal and caoutchouc, as incense to the idol of the god who was held to be protector of hunting and fishing. When the dance was finished, the head and feet were scorched in the fire before the idol, as an offering, and afterwards taken to the house of the high-priest and eaten. The flesh and blood were then eaten before the idol; and the same was done with all the animals which they offered in sacrifice. When they sacrificed fish, the entrails were burnt before the idol.

When a woman was in travail, the midwives made her confess her sins; but if this was not sufficient to hasten the birth, they made her husband do the same; and finally, if the woman admitted illicit connection with any other man, they went to his house and took his clothes and placed them beneath her; if this failed, as a last resort, the husband sacrificed blood from his tongue and ears. When the child was born, if a boy, they put in his hands a bow and arrows;

if a girl, a spindle of cotton; and the mother made a streak of soot mixed with water on the right foot of the child, which they believed would prevent it, when grown up, from being lost in the woods. At the end of twelve days, the child was taken to the priest, green branches being scattered under the feet of the bearers. The priest gave it the name of its grandfather or grandmother, as the case might be, and they presented it with cacao and fowls, which were the offerings made to the priest. When it was taken back to the house, the mother carried it to a river and bathed it, offering to the stream, cacao and copal, that it should never do evil to the child.

As regards the rites for the dead; if the defunct were a cazique or captain, or the wife or child of either, all the people mourned for four days and nights. At the rising of the sun on the fifth day, the high priest announced that the soul of the dead was with the gods, and that it was useless to mourn any longer. They buried the dead man dressed in all of his riches, in a sitting posture, and in his own house. Their manner of mourning during the four days and nights resembled a *mitote*, in which they chanted the lineage and deeds of the dead. If he were a cazique who died, the high priest and all the people, immediately recognized as his successor his son or daughter; or, if he had neither, his brother or nearest relative.

On such occasions they had great feasts, dances and sacrifices, and the new chief entertained in his house all the priests and captains. If a common man died, only his children and relatives mourned; and if a woman lost her child, she reserved her milk for four days, without giving it to another; for they believed, if she failed in this, the dead child would do the living one some injury. This sacrifice they called *navitia*.

It was the office of the *cacique* to order the plantings, and direct the marriages. They always married when young; and when the affair was arranged, and the affianced groom met his future father-in-law he turned aside, as also did the affianced bride when she met her future mother-in-law. They did this, because the devil had made them believe that such encounters would prevent their having children. Marriages were celebrated in this wise: the male relatives of the woman sought the bridegroom and made him bathe in a river; and the female relatives of the woman did the same with the bride; they then wrapped each of them in a new, white cloth, and took them to the house of the bride, where they tied them up naked, in their garments. The relatives of the young man then made presents to the bride of cloths, cottons, fowls and cacao, while those of the bride gave presents of the same kind to the bridegroom; after which they all feasted together. At these marriages the high priest and *cazique* were obliged to be present.

Concerning relationship: They have a tree painted, with seven branches, which represent the seven degrees of relationship in direct descent, within which no person might marry, excepting those who had distinguished themselves in war, but even these might not marry within three degrees of blood. In respect of the line collateral, they made use of another tree with four branches, which represented the four degrees within which no one could marry.

Aside from other laws which these Indians possessed in common throughout the province, those of this nation have the following as inviolable:

Whoever contemned or ridiculed the sacrifices to the idols, or the ceremonies connected therewith, was condemned to death.

Whoever had connection with a strange woman, was condemned to death.

Those who had carnal intercourse with relatives, within the degrees above proscribed, both suffered death.

He who spoke libidiously with a married woman, or who made improper signs to her, was banished and his property confiscated.

Whoever had commerce with a strange slave (one not his own ?) was himself reduced to slavery, unless pardoned by the high priest for services in war.

Whoever wounded another, if the wound were serious, suffered death therefor.

Whoever violated a virgin was sacrificed.

Whoever lied was severely whipped; and if it were in any matter concerning war, he was enslaved.

Those of the people who were not soldiers cultivated the plantations of the cazique, pontiff and priests; and also gave a part of their own crops for the support of the warriors.

This is what I have been able to gather concerning the manners and custom of this people.

Near this place, is a high rocky hill from which flow two streams of water, close to each other, one hot and the other cold. Here too is found an abundance of spices, which the Indians use in their drink and food; and an earth which resembles copperas, and which it must be judging from its effects. With this they make a dye.

From here to the borders of the province of Chiquimula de la Sierra, the country is for the most part high, of good temperature, abounding in pasturage, and adapted for the support of cattle, and the cultivation of all kinds of grains.

In the portion of this province which lies in the direction of Gracios á Dios in Honduras, are the Chontal Indians. While there, complaint was made to me against a cazique of a place called Gotera, who since the time of his paganism had had his private member split open, as was the custom anciently, among the most valiant. In 1563, certain idolatrous Indians of another village called Cezori, got together in a neighboring forest where one of them performed the same operation; and afterwards they circumcised four boys of twelve years of age, in the Jewish manner, offering the blood to an idol of stone of a cylindrical form, with a double visage and many eyes, called Icelaca. They say that he is the god which knows the present and the past, and sees all things. Both his faces were anointed with blood, and they sacrificed to him deer, fowls, rabbits, peppers, and other things which they used in ancient times.

Torquemada (1723, lib. 3, cap. 41, vol. 1, p. 330) has recorded a Lenca myth which, he says, was told him by the old people. According to them, 200 years before this time, there came to Cerquin (Lehmann states, 1920, vol. 2, p. 636, that this was probably Corquin in the Department of Gracias, Honduras), a lady, white as a Castilian, whose name was Comicalual, meaning "jaguar that flies", so named because she was very wise and versed in supernatural arts. These Indians held the jaguar in high esteem. She made her abode in Calcoquin, which was the most fertile land in the province. Here there were stone "lions" which they worshiped, and a large three-pointed stone which had on each point three grotesque faces. Some said that Comicalual carried it there through the air and by its virtue

won battles, thus extending her realm. Some said that she had three supernaturally conceived sons, others said they were her brothers. When she grew old, she distributed her territories among them with advice concerning the good treatment of her subjects. She then commanded that her bed be taken out of the house. Lightning flashed and thunder roared. The people saw a beautiful bird flying across the sky and, as they never saw the lady again, they believed she was the bird and thus went to the sky. The sons (or brothers) divided the realm and governed it well. The people were courageous and warlike. They had been taught religion and enchantments by the Lady Comicahual. Among the many idols which they adored, there was one called the Great Father and another called the Great Mother. To these idols they prayed for their well being. Other gods were introduced, to whom they prayed for food, property, riches, and that their lands might prosper, and produce abundantly. And, "for many years these superstitions and deceits of Satan lasted among the old people." Lehmann (1920, vol. 2, p. 637) is inclined to identify the Calcoquin of Torquemada with the Icelaca of Palacio. He goes on to show that similar rites, presumably originating with the Pipil as indicated by Palacio, extended as far north as the Bay Islands in the Caribbean. This evidence, derived from Salcedo, has already been cited elsewhere (Strong, 1935, pp. 14, 15) and need not be repeated here. Sufficient for our present purposes is the fact that elaborate but basically similar cult observations extended from Salvador north beyond the mouth of the Ulua River and that many of these at the time of the Conquest seem to have originated in Pipil territories. Only the results of scientific archeology can show whether this historic Salvadorean center was actually primary or was derived from still earlier sources of cultural development. This will be discussed in relation to the results of our own archeological excavations.

Linguistically, the Lenca and the Jicaque have since been studied by various travelers. This material has been summed up and amplified by Lehmann (1920, vol. 2, pp. 649-722). From the ethnographic standpoint, recent work on the Lenca and Jicaque has been pitifully inadequate. Habel (1880) describes various Jicaque he met in the Department of Yoro as follows:

The Xicaques differ in the form of their bodies from all the other tribes of Central America. Their stature, on the average, being equal to that of Europeans, is greater than that of the other tribes. Their skin is of a lighter color, and their features resemble more closely those of the Caucasians, having a more pleasant and intelligent expression than any other tribe of this region known to me. Both sexes wear a kind of apron made of the inner bark of the Caoutchouc tree. That of the women reaches around the waist and the ends hang down

from the hips to the knees. These two flaps are attached to the body by a strap of the same material fastened around the waist. By another narrower strap, tied around the head, they secure the long black hair, parted in front, floating down to the shoulders.

According to Habel, the Jicaque had but recently been gathered into permanent settlements through the splendid efforts of a Spanish missionary. He adds that they were improvident, did not cultivate the soil nor raise any large domesticated animals. They had formerly been permitted to sell themselves into practical slavery, but this practice had then been stopped. They traded in sarsaparilla and tobacco. Habel goes on to discuss the physical and other characteristics of the still numerous Paya, who appeared to him to be much darker in pigmentation than the Jicaque. We have previously indicated that quite primitive groups of Jicaque survive at the present time.

According to Otis T. Mason (1889), the Lenca of Honduras had an ingenious method of straightening lance shafts. A pole about 16 feet long was suspended vertically from the limb of a tree by a lariat attached by half hitches to both ends of the pole. At the lower end, the lariat was attached to a rock weighing around 50 pounds, the shaft being thus held straight while seasoning. He goes on to describe a variant of the musical bow used by the Lenca which was called a "bumbum." This strung bow had a small gourd on the back of the bend which was attached to the bow cord by another string running at right angles. The bow was rested on a half gourd inverted on the ground, which gave added resonance while playing (Mason, 1889). Apparently this instrument was not confined to the Lenca, for Habel (1880, p. 31) describes an identical instrument used at about the same time by the Pipil of the Balsam Coast of Salvador. Here it was strung with wire and called the "carimba." The melody was produced by strumming the wires with a stick and cupping the hand over the gourd. Quite possibly this represents a variant of the musical bow, or it may be a historic borrowing from the African marimba so popular in Central America at present. Whether it is primarily of New World or of African origin, we cannot say.

In June 1936 the junior and senior authors of the present report were grounded by an airplane accident at the town of San Pedro Sula in Honduras. While waiting for a track car, we were entertained by a small native boy who, with a short stick, strummed dolefully on the identical instrument described by Mason. In this case the bow string was of wire and the bow rested on an empty carton instead of a gourd.

Squier (1859, pp. 603-619) gives a brief but vivid picture of a fiesta at Comayagua in which Indians from the nearby mountains performed dances accompanied by much ceremonial drinking and native ritual. The deer and the ocelot were the symbols of the two main dancing groups. Their musical instruments consisted of flutes, the Panspipe, the marimba, and a covered pot with a string drawn through the bottom. At this fiesta, the Indians, the majority of whom were probably Lenca, visited the numerous ruined towns in the vicinity of Comayagua that had been occupied at the time of the Conquest. He also described an extremely isolated village of the Guajiquero Lenca and gives an amusing account of the difficulties involved in securing linguistic or ethnographic information from the Indians. As anyone knows who has attempted work with Honduras Indians, the repression of almost half a millennium combined with linguistic barriers is not an easy thing to overcome. However, it is obvious from Squier's account that a wealth of native custom and belief still survives among the more isolated groups.

Such survivals, combined with the extremely haphazard nature of previous research among the living Indians, indicate that there is much more information available in Honduras for the trained ethnologist and linguist than has been generally realized.

EARLY HISTORIC CONTACTS IN NORTHWESTERN HONDURAS

The fourth voyage of Columbus gives us our first historic glimpse of conditions on the Honduras mainland. Having visited the Bay Islands, Columbus landed at Punta de Caxinas (the Cape of Honduras) on August 14, 1502. The chroniclers of this voyage give a brief but vivid picture of the advanced agricultural life and the thriving coastal trade then existing on the north coast of Honduras.⁷

In 1524 Gil Gonzalez named Puerto Caballos (later to become Puerto Cortez) and established a settlement at San Gil de Buena Vista. From this base he sailed down the coast and marched overland into the Olancho valley, where he met and defeated a force under Hernando de Soto that had been exploring this region from Nicaragua. Returning to Puerto Caballos he was informed of the arrival of a Spanish fleet under Cristobal de Olid.

It is of interest that again Honduras becomes a buffer area and battleground between two earlier established southern and northern

⁷ Pertinent historical and ethnographic information regarding the Bay Islands and the adjacent mainland have been given elsewhere (Strong, 1935, pp. 7-19). The following historical résumé of the Ulua region is primarily condensed from Bancroft, *History of Central America*, vols. 1 and 2, 1883. Other sources are cited as they occur.

centers, the one in Panama under Pedrarias, the other in Mexico under Hernando Cortez. Not content with the rich spoil of the Aztec Empire, Cortez had already cast covetous eyes to the south where rumor painted the golden glories of Hibueras or Honduras. For this reason he despatched a trusted lieutenant with a fleet to conquer the province. Having already reached an agreement with Velasquez, Governor of Cuba and the rival of Cortez, Olid, in 1524, established the settlement of Triunfo de la Cruz east of Puerto Caballos and withdrew his allegiance from Cortez. The latter countered by dispatching another fleet under Las Casas, which proceeded from Mexico to the Bay of Honduras. Olid promptly attacked Las Casas. As Bancroft says, "it was an original spectacle in these parts, Spaniards fighting Spaniards, in regular naval engagement; and as the hissing projectiles flew out from the smoke over the still waters, followed now and then by a crash, the noise reverberating over the forest-clad hills, the dusky spectators should have been exceedingly grateful for this free exhibition of the wisdom and power of European civilization that had come so far to instruct them in such a fashion."

Although the honors of battle, if any, went to Las Casas, a tropical storm wrecked his fleet and he was forced to surrender. Along with Gil Gonzales, who had also been captured by Olid, Las Casas was taken inland to Olid's headquarters newly established in the large Indian town of Naco (see maps, figs. 1, 2). Here, although they were treated as guests by their captor, the two captives plotted against Olid, and eventually cut his throat with a table knife. Crawling away into hiding, Olid sent for a priest. The latter being followed, Olid was dragged into the plaza at Naco and publicly beheaded. Las Casas returned to Mexico by an overland route through Guatemala. Even today, over 400 years later, a tradition still persists among the unlettered inhabitants of present-day Naco that here "the king was killed" after being dragged in from his hiding place at El Salto, the falls of the beautiful little Naco river. Here, as elsewhere in the New World, European civilization was ushered in with blood and treachery.

Meanwhile Cortez had had no word from his latest Honduras venture. Despite the advice of his other lieutenants, he decided to leave Mexico and proceed overland to Honduras.⁸

⁸ The best sources on this amazing expedition are given in Maudslay's translation of Bernal Diaz, "The True History of the Conquest of New Spain, vol. 5", 1916. The pertinent letters of Cortez to the Emperor Charles V are also included in this volume.

It is of interest that before starting, Cortez obtained maps from the Indians of the Vera Cruz region showing the entire area between that point and Panama. It is apparent that he was traveling along well-known aboriginal trade routes throughout most of his journey, and he mentions that nearly all the towns he stopped in were full of traders. The details of his Yucatan traverse do not particularly concern us here until he arrived at Nito near the Gulf of Dulce. Here he found the diseased, starving remnants of Gonzales' colony. Making an expedition up the Gulf of Dulce, Cortez captured a well-provisioned pueblo and obtained supplies for continuing his journey. From Nito, Cortez proceeded by sea to the vicinity of Puerto Caballos, where he established a settlement. He sent Sandoval overland to Naco. After crossing the Motagua River and visiting several pueblos, Sandoval's force arrived at Naco. The town had been recently deserted by its native inhabitants but contained abundant provisions and even salt; and here the Spaniards settled themselves, in the words of Bernal Diaz, "as though we were going to stay there forever." In a later section on the excavations at Naco, we will give more details regarding native conditions in the vicinity of Naco at the time of Sandoval's visit.

Regarding the probable linguistic affiliations of the natives of Naco and the adjacent pueblos, it is significant that Lehmann lists three pueblos mentioned by Bernal Diaz "in the neighborhood of Naco" as having Nahuatl names.⁹

Similarly, Cortez states:

When I first arrived at this pueblo (San Andrés), I heard from the Spaniards who had come from Naco that the natives of that pueblo and of the neighboring pueblos, were somewhat disturbed, and had left their houses for the hills and forests, and that although some of them had been reasoned with they refused to be pacified from fear of the treatment that they had received at the hands of the followers of Gil Gonzalez and Cristobal de Olid. I wrote the Captain in charge there and told him to do all that he could to capture some of the natives by whatever means he could devise, and to send them to me so that I could speak to them and reassure them. This he did, and he sent me certain natives whom he had captured during an expedition which he had undertaken, and I talked to them and gained their confidence, and let them talk with some of the native Chiefs from Mexico, whom I had brought with me. These Chiefs told them who I was, what I had done in their country, and what good treatment they had received from me when once we were friends, and how they were protected and governed in justice—they and their property, their wives and children—and the punishment that those received who rebelled against the service of your Majesty, and many other things which they told them. After this,

⁹ Lehmann, 1920, vol. 2, p. 1018. Also see Nahuatl distributions on linguistic map.

they regained confidence, although they still told me that they had some fear that they were not being told the truth, for those captains who had come in advance of me had told them the same things and more to the same effect, and that they had lied to them and had carried off their women when they had sent them to make bread, and that the men who accompanied them had been forced to carry loads, and they believed that I would do the same. Nevertheless, with the assurances which the Mexicans and the Interpreter (Marina, a Mexican woman) whom I had with me gave them, and seeing those of my company happy and well treated, they were somewhat reassured. I sent them off to speak to the Chiefs and people of the pueblos, and in a few days the Captain at Naco wrote me that some of the neighboring pueblos had become peaceful, particularly the chief pueblos which are: Naco, where the Spaniards are residing, Quimiztlan, Sula and Tholoma (Cheloma)—the smallest of these had more than two thousand houses—and other villages which were subject to them; and that the envoys said the whole country would soon be at peace, for they had sent messengers to pacify the people, telling them of my arrival among them and all that I had said to them, and also what they had heard from the natives of Mexico; they added that they greatly desired that I would go to Naco, as my arrival there would give confidence to the people. This I would have done with good will, had it not been very necessary for me to continue my journey in order to arrange that which I shall explain to your Majesty in the following chapter.¹⁰

From the foregoing it seems quite possible that the people of Naco spoke a Nahuatl dialect understandable to the Aztec caciques and to Doña Marina, Cortez' famous Mexican Indian woman interpreter. Had the temporary captives from Naco been Jicaque, Lenca or Maya, this would not have been possible. It is also possible that certain Nahuatl dialects served as a *lingua franca* in the area, due to the obviously extensive trade connections then in existence with Mexico and to the extent of Pipil influence exerted from Salvador. However, elsewhere Cortez mentions linguistic difficulties when entirely alien languages were encountered by his men, but this does not seem to have been the case here.

Cortez then proceeded by sea to the newly founded town of Trujillo. His settlement near Puerto Caballos was soon abandoned, owing to sickness and lack of food, in favor of Naco. A number of large and rich pueblos in this vicinity were gradually conciliated by Sandoval, but the inhabitants of Naco, owing to the severe treatment they had received from Olid, refused to return to their homes. While Sandoval was at Naco, the caciques of two pueblos named Quespan and Talchinalchapa came to him to report the depredations of some other Spaniards who had arrived from the South.¹¹ These were seized and proved to be a party under Garro from Nicaragua that had been

¹⁰ Bernal Diaz, 1916, vol. 5, p. 407, from the fifth letter of Hernando Cortez to the Emperor Charles V; also see p. 60.

¹¹ Bernal Diaz, 1916, vol. 5, p. 66.

sent to claim the lands to the north for Pedrarias. They were well equipped with arms and horses and had handsome Nicaraguan Indian women with them. Sandoval sent them under guard to Cortez at Trujillo. Bernal Diaz, who was with this overland party, describes the difficulties and the Indian fights they encountered. Unless one has actually traveled through these mountainous, tropical countries, it is impossible to appreciate how truly amazing such early Spanish journeys were. Even today an overland trip from Naco into Nicaragua would be an expedition not to be undertaken lightly. Yet in the time of Cortez, Spanish adventurers seem to have already traversed the Central American cordilleras from end to end. Cortez returned Garro to Nicaragua with messages of good will and mining supplies. For some time Cortez toyed with the idea of adding Olancho and Nicaragua to his conquests and even went so far as to start a road from Trujillo to Nicaragua! However, a mission from Mexico arrived with bad news, and the road is still unbuilt.

Hearing that his holdings in Mexico had been seized by enemies, Cortez determined to return at once. Before departing he ordered Luis Marin with a number of discontented colonists from Trujillo to proceed to Naco where there was abundant good land. Saavedra, who was then campaigning in Olancho, was to remain as Governor of Honduras. After a hard trip Marin arrived at Naco, and the next day, in company with Sandoval, set out on the overland trip through hostile Guatemala to Mexico. Meanwhile Cortez, who, strange to say, appears to have been a very bad and timorous sailor, had been driven back by storms. Messengers were sent to Sandoval ordering him to stop and settle. This was a great blow to the overland party, for they desired above all else to return to Mexico. Sandoval hurried to Trujillo to plead with Cortez, that he set sail and let the overland party proceed. Under Marin the latter went "to some pueblos called Maniani and thence to another pueblo named Acalteca, where at that time there were many houses."¹²

Despite Sandoval's plea, Cortez still refused to sail. Sandoval was dispatched to Olancho where he drove out Rojas, a lieutenant of Pedrarias. On Sandoval's return, Cortez sent orders to Marin to proceed, and he ordered Godoy, who was forming a settlement at Puerto Caballos, to go to Naco with all his people. Finally, in 1526, Cortez set out for Cuba and, eventually, Mexico.

Finally, Pedro de Alvarado, having received orders from Cortez to proceed from Guatemala to Honduras, began his march. Marin,

¹² Bernal Diaz, 1916, vol. 5, p. 86.

desperate and without orders, sent a party of 10 men through Olancho to go to Trujillo. According to Bernal Diaz, they got as far as the gold-working region on the Guayape River, when they learned of Cortez' departure. Receiving orders from Saavedra to return, they did so, and, Bernal Diaz remembers, they threw stones at the country as they left. They met Marin at the pueblo of Acalteca and then proceeded to another pueblo called Maniani, where they encountered six of Alvarado's soldiers. In two days' marching they reached Alvarado "near the town called Chuluteca Malcala." This was probably the site of Tegucigalpa on the Choluteca River. From here the combined parties proceeded toward Guatemala after a difficult crossing of the Lempa River, which was then in flood.

Years later, Bernal Diaz (1916, vol. 5, pp. 328, 329) thus recalled the country of Naco and of the Ulua River, as it was when he first saw it and as it soon became :

and what I state I know, for when I came with Cortés on the expedition to Honduras I was present in Trujillo, which was called by the Indian name of Guaimura, and I was at Naco and the Rio de Pichin, and that of Balama, and that of Ulua, and in nearly all of the pueblos of that neighborhood, and it was thickly peopled and at peace (and the people were living) in their houses with their wives and children; but as soon as those bad governors came they destroyed them to such an extent, that in the year fifteen hundred and fifty one, when I passed through there on my return from Castile, two Caciques who had known me in the old days, told me with tears in their eyes of all their misfortunes and the treatment (they had received), and I was shocked to see the country in such a condition.

The details of this tragic and complex period in Honduran history cannot be considered here. The withdrawal of Cortez threw the new colony into turmoil and the starving colonists engaged in every form of intrigue. Coming from Guatemala, Pedro de Alvarado took over the governorship and set about pacifying the country. He built the town of San Juan at Puerto Caballos and founded San Pedro. For the Indians this was an even more tragic period. According to Bancroft (vol. 7, pp. 233-234) Indian slaves were kidnapped and sold in Honduras by the shipload. In the vicinity of Trujillo where there had been villages of from 600 to 3,000 houses, there were not more than 180 Indians left in 1547. Those not enslaved or killed had fled to the mountains. At Naco, where there had originally been a population of about 10,000, there were, in 1536, only 45 remaining. At La Haga, a coastal town some 9 leagues from Trujillo, there had been about 900 houses, but of the entire population, only the daughter of the Cacique remained. The cruelty toward the natives was even greater than in Guatemala. In 1539, when Alvarado returned from Spain

and transported the materials for building a fleet across the isthmus, the entire remaining Indian population fled. These evils were presented in full detail by Bartolome de Las Casas, and the new laws resulting from his famous publication at least gave nominal protection to the oppressed natives.

In answer to a petition from Trujillo, the Emperor appointed Francisco de Montejo, the former governor of Yucatan, as ruler of Honduras. Only a handful of starving Spanish colonists remained. Montejo subdued but did not enslave the Indians of the mountains near Trujillo. Many Indians returned voluntarily to their homes in this region. Montejo then visited the town of Gracias á Dios. Here, owing to the murder of a Spaniard, he arrested and punished the Lenca Indian ring leaders in the presence of the Caciques of the district of Cerquin previously referred to. This aroused the opposition of the famous Lenca leader Lempira, "Lord of the Mountains." Lempira had previously withstood Alvarado and driven off Spanish attacks under Chavez, and he now opposed Montejo. The great Indian leader had secured allies from various interior tribes including several that had formerly been hostile to the Lenca, and was estimated to have a force of some 30,000 warriors.

According to Lehmann (1920, vol. 2, p. 637), he had united the men of more than 200 towns and commanded over 2,000 "men and gentlemen of distinction."

"Lempira, the last of the chiefs of Corquin, made his final stand against the Spaniards on the mountains of Piriera, which overlooks the valley of the river Lempa, in the name of which beautiful stream his own is commemorated." (Squier, 1858, p. 329.)

Here for 6 months he was besieged by Caceres, a lieutenant of Montejo, but so greatly were the Spaniards harassed by the Indians that they were on the point of failure. Siege and assault having failed, Caceres resorted to treachery. Under a flag of truce Lempira came to the walls of his stronghold to parley with his enemies and was shot by a hidden marksman. The Lenca and their allies fled, and the great conspiracy soon fell to pieces.

Mrs. Popenoe, quoting from a letter from Montejo to the King of Spain, June 1, 1539, gives the following account of the latter part of this campaign against the Lenca: ¹³

Disturbing news reached Gracias, where Montejo was sojourning with 11 Spanish soldiers. The Indians were preparing stubbornly to resist him. In Yamalá, a nearby village, they were building many houses on a great, very

¹³ D. H. Popenoe, 1936, pp. 559-560. For the original, see *Colección de Documentos Inéditos*, 1864, vol. 2, pp. 212-266.

strong rock which they have, and providing them with provisions. The Spanish chieftain sent a Negro spy, who knew the language of the Indians, to enter the stronghold and bring back a report. The frightened Negro found there four houses built very large, and four more larger ones full of corn, and he set fire to the houses and to the corn. Word came of a great disaster in the valley of Comayagua. The Indians had risen. One Spaniard had been killed and several others wounded. Four horses had been lost. Unable longer to withstand the siege, the Spaniards had fled at night to a neighboring province where the inhabitants were friendly.

Montejo realized that the time had come for desperate action. Supplies were brought together, and soldiers were called in from regions where the danger of rebellion was not imminent. Others who had been wounded but now had recovered sufficiently to join the colors, augmented the small band which was placed under the leadership of Alonzo de Cáceres, recently returned from the final campaign against Lempira.

When they arrived at Comayagua they found that the Indians, doubtless apprised of their approach, with all available supplies would fortify themselves on big rocks. Cattle which they could not take with them had been killed and eaten, so that the valley was now in a state of starvation.

Montejo advanced into one part of the valley, Cáceres into another, attacking and capturing a mountain fortress "which was the strongest in that region." The last named leader then proceeded to a village, by name Guaxerequi, where six Christians had recently been killed. There he found another fortress. At this point he was rejoined by Montejó, who describes the place in his letter. He says: "and (has) seen (or visited) a great rock, which was the strongest thing that has been seen, which, if they had time to cut a ridge of mountain, which they were cutting, would be impossible to capture, for they had on it water and wood and cultivated fields and many provisions; they had 220 large houses, and certain temples and places of worship."

It took the combined forces of Montejó and Cáceres four months to conquer the valley of Comayagua, after which they carried the campaign into Olancho.

Such stories as the above throw much light on the importance of fortified mountain tops at the time of the Conquest. Although it has been impossible to place Tenampua (the famous archeological site near Comayagua, first described by Squier, 1858 and 1869, see map, fig. 1), among the strongholds described in the early accounts at my disposal, it seems probable that it may have been one of those captured during the campaign carried out in the Comayagua region by Francisco de Montejó and his lieutenant, Alonzo de Cáceres. It may have been the formidable Guaxerequi described in Montejó's letter.

In the light of the partially cut "cuchillo" or narrow neck connecting Tenampua with the main promontory to the northeast (D. H. Popenoe, 1936, pp. 562, 563 and map), I am inclined to believe that this identification of Guaxerequi and Tenampua is indeed very probable.

It is certain that a complete combing of the sources, combined with first-hand examination of the available archives in Honduras and neighboring countries, would yield a considerable mass of information on the Lenca and their neighbors, but this is not possible at

present. All that has been attempted here is to suggest the main trends of a fascinating historical period and to indicate the probable distribution of ethnic groups in the region under investigation. We turn now to outlining the results of direct archeological research.

ARCHEOLOGICAL EXPLORATIONS

CHAMELECON RIVER

Our reconnaissance of the middle Chamelecon River extended from May 26 until June 17, 1936. It was aimed primarily at Naco but several other sites were also investigated. Through the courtesy of the United Fruit Company we lodged comfortably at Manacal Ranch (map, fig. 2) which is located about a mile south of the town of Cofradia. Here we obtained horses and mules and were thus able to work at a number of archeological sites in the general vicinity. We first visited the San Luis site just above the confluence of the Naco and Chamelecon Rivers (map, fig. 2). Next we spent 2 weeks mapping and digging exploratory trenches at Naco. The remainder of the time was occupied in making stratigraphic sections and maps at the prehistoric Las Vegas and Tres Piedras mound sites.

NACO

All Honduras records of the Conquest refer to Naco, first as a thriving Indian town and later as the site of repeated Spanish settlements. The Indian pueblo of Naco was only one of a considerable group in the vicinity. Montejo states that the original population of Naco was 10,000 persons (*Collección de Documentos Inéditos*, 1864, vol. 2, p. 228), an estimate that agrees reasonably well with the previously cited statement of Cortez that the smallest of the pueblos in that vicinity had more than 2,000 houses. Las Casas, speaking of Honduras, says: "Tenia Pueblos innumerables, y una vega de treinta leguas y mas, toda muy poblada . . . la ciudad de Naco que tenia sobre doscientas mil animas, y muchos edificios de piedra, en especial los templos en que adoraban" (cited by Bancroft, *Native Races*, vol. 4, p. 77). When compared to the other authorities, as well as to the size of the ruins, this would seem to be an extremely exaggerated estimate. Similarly, his statement (*Las Casas*, 1822, p. 45) that between the years 1524 to 1535 more than 2,000,000 Indians perished in the kingdom of Naco and Honduras, leaving only 2,000 inhabitants in a territory 100 leagues square, must be taken with a large grain of salt. Diaz, Montejo, and others give ample proof that the natives of Honduras were cruelly despoiled and that whole districts were de-

populated in the early days of the Conquest. Nevertheless, the wholesale statistics of Las Casas seem to be those of a crusader rather than a historian.

Bernal Diaz (1916, vol. 5, pp. 56-59) gives a first-hand picture of Naco as it was in 1525.

At the hour of Mass we went to Naco. At that time it was a good pueblo, but we found it had been deserted that very day, and we took up our quarters in some very large courts where they had beheaded Cristóbal de Olid. The pueblo was well provisioned with maize and beans and Chili peppers, and we also found a little salt which was the thing we needed most, and there we settled ourselves with our baggage as though we were going to stay there forever. In this pueblo is the best water we have found in New Spain, and a tree which in the noonday heat, be the sun ever so fierce, appears to refresh the heart with its shade, and there falls from it a sort of very fine dew which comforts the head. At that time this pueblo was thickly peopled and in a good situation, and there was fruit of the Zapotes, both of the red and small kind, and it was in the neighborhood of other pueblos.

. . . When we arrived at the Pueblo of Naco and had collected maize, beans and peppers, we captured three chieftains in the maizefields and Sandoval coaxed them and gave them beads from Castile, and begged them to go and summon the other caciques and we would do them no harm whatever. They set off as they were ordered to do, and two caciques came in, but Sandoval could not induce them to repeople the pueblo, only to bring a little food from time to time; they did us neither good nor harm, nor we to them, and thus we continued for the first days. . . . When Sandoval saw that the neighboring Indians and natives of Naco did not want to come and settle in the pueblo, although he sent to summon them many times, and that the people of the neighboring pueblos did not come or take any notice of us, he decided to go himself and manage to make them come. We went at once to some pueblos called Girimonga and Açula, and to three other pueblos near Naco, and all of them came to give fealty to His Majesty. Then we went to Quimistan [Quimistlan in preceding chapter, Quimistan on map] and to other pueblos of the Sierra, and they too came in, so that all the Indians of that district submitted, and as nothing was demanded of them beyond what they were inclined to give, their submission did not weigh on them, and in this manner all was pacified as far up as to where Cortés founded the town which is now called Puerto de Caballos.

Modern Naco is a small village of perhaps a dozen mud-walled and thatched houses on the beautiful little Naco River. Permission to excavate was kindly granted us by the son of the owner, Dr. Paz Barraona, and by Don Santiago Nolasco, the head man of the village. Don Santiago and the other residents of Naco were interested spectators or laborers during our work here and the children brought us many fragmentary specimens from the adjacent river banks. The heart of the site is still covered by the small but very dense shade trees mentioned by Bernal Diaz. These shaded our work but made mapping difficult. Noontime siestas spent under great jungle trees

bordering the rapid, sparkling, Naco River made us appreciate the remark of the soldier-historian that "here is the best water we have found in New Spain."

It is not the purpose of the present report to discuss fully the excavations at each site nor to analyze the archeological findings in any detail. Instead, a brief summary of significant excavations will be given, and at least one stratigraphic or horizontal artifact record at each site will be outlined in an effort to indicate the apparent trend of local cultural development. This preliminary analysis will be confirmed or amended in the final report in accord with the full statistical findings and in relation to all the excavations. Although no numerical record of artifact or ceramic types is given at this time, an effort has been made to discuss them quantitatively rather than selectively. In regard to ceramics, which greatly preponderate over any other artifact types throughout the entire Uluá drainage, we have here attempted to suggest the relative proportions of all wares at each site or in each stratigraphic section discussed. When the very extensive sherd collections of the expedition have been analyzed and the data fully presented it will be possible to check this preliminary analysis against the complete record. In regard to technical names applied to various soil layers these have been used in a very general sense. When our soil samples have been fully studied by experts it may be possible to supplement the cultural record with the detailed findings of soil analyst and sedimentation expert.

As previously indicated, the ruins around Naco are extensive, and our detailed survey deals with only the central area. The map (fig. 3) gives the essential data in regard to mound orientation and elevations. In general, the Naco mounds are low and rounded, apparently forming the foundations of houses, but the group just northeast of the ball court differs in this regard. Mound 6 appears to have been the center of the complex. It is still the highest and was, in all probability, originally faced with squared stones, forming a square-faced pyramid with a flat top (fig. 3). A few of the cut stones are still in place. It has been sadly damaged by the disruptive effects of tree growth. According to local authorities it has also suffered by an earthquake, by having its stone facing removed for road foundations, and, about 1902, by treasure-hunting excavations. It is still quite impressive, however. Mound 6 is flanked by mounds 3, 4, 5, all of which are exceptionally large. To judge by mound 3, which we cross-sectioned near its southern end (fig. 4), mounds 3 and possibly 5 were originally capped by thick white plaster. This had eroded off the steep sides of mound 5 but was present at the base and over the flattened

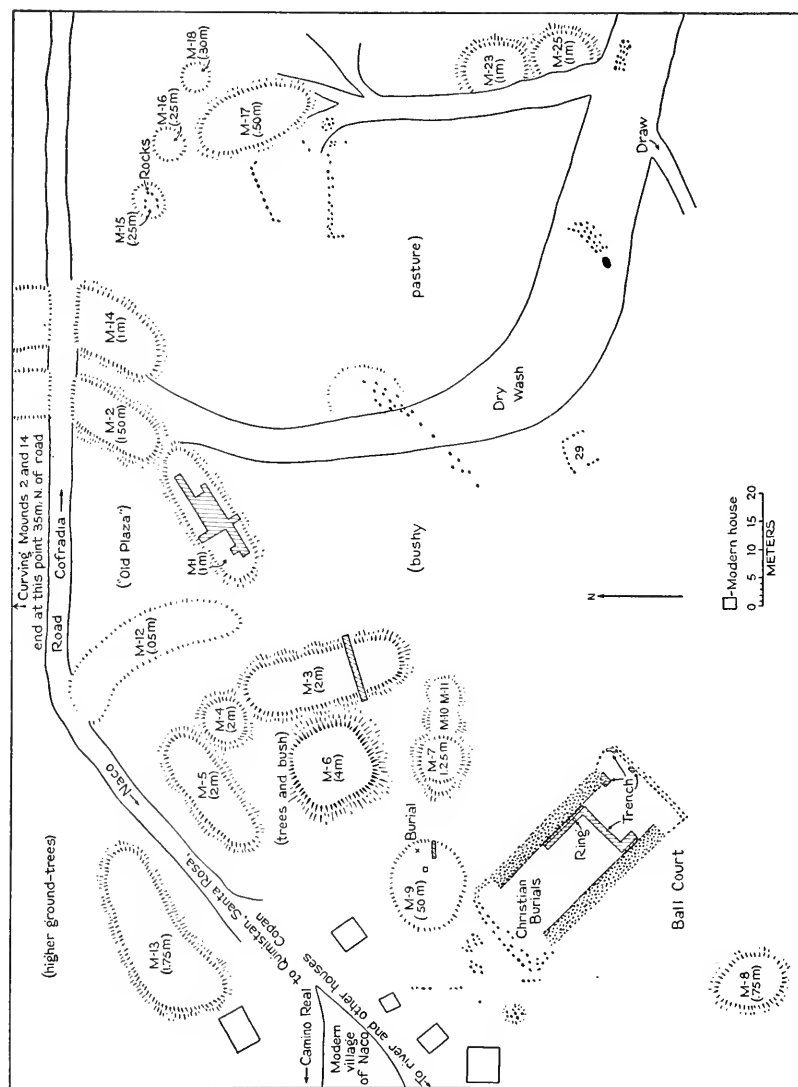


FIG. 3.—Sketch map of the ruins of Naco.

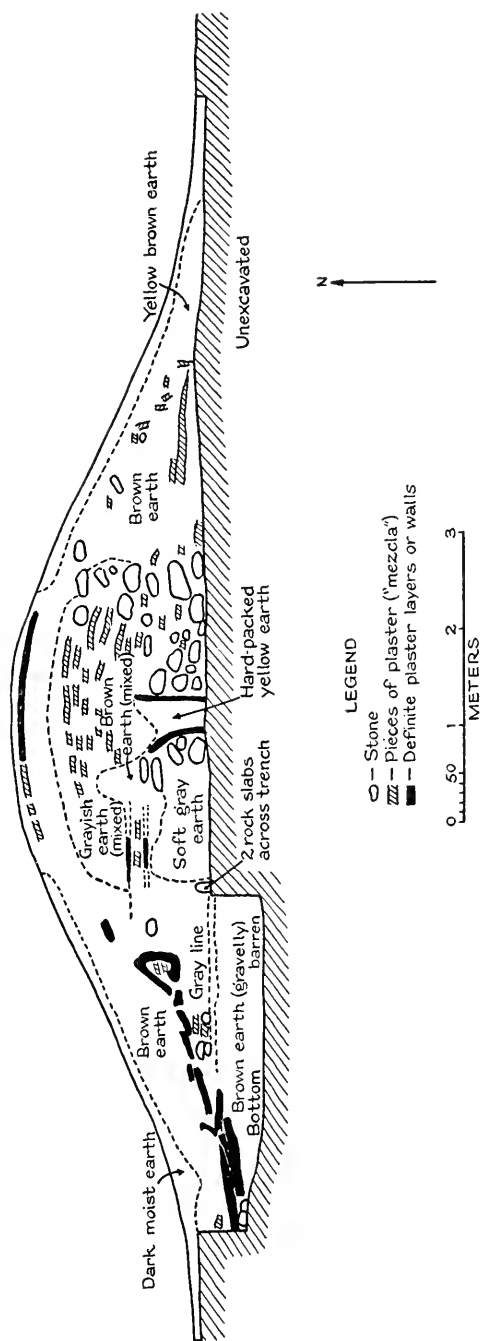


FIG. 4.—North wall of cross-section trench through mound 3, Naco.

top (fig. 4). Mound 3 included an inner structure the nature of which could not be satisfactorily determined by our one cross trench. This occurrence of two thin plaster walls running through the heart of the mound is shown in the illustrations (pl. 1, 2 and text fig. 4). A small trench in mound 9 (fig. 3) revealed aboriginal refuse and disarticulated human remains. Owing to its proximity to certain historic burials, work here was discontinued.

Horizontal stripping of mound 1 (fig. 3) revealed considerable portions of the floors of two houses with massed small boulders on the north side and tumbled adobe blocks on the south side (Strong, 1936, fig. 68). The plastered floors were stained a rich, dark red. Fragments of plaster apparently from the walls showed five successive layers of red, yellow, red, blue gray, and red indicating the varying washes used in decorating the interiors of the houses. These colors were very fresh when uncovered but have since faded slightly. To judge from our test cuts, these long, low mounds north of the central pyramid complex consist of rows of house floors. Owing to the curve of mounds 2 and 14 (fig. 3) they enclose a crescentic area which may have been the old plaza of Naco. Our excavations, although very incomplete, indicate that with adequate time a whole series of house floors could be easily cleared. The earth covering them is shallow, and the floors are intact. Such work would be of the greatest value in revealing actual living conditions in aboriginal Naco. When the potsherds from inside mound 1 were being washed, we encountered two pieces of European glazed crockery. One of these (pl. 4, *m*) was obviously an early Spanish piece, the other might possibly have been intrusive from more recent times. Since it was in these houses that Olid, Bernal Diaz, and other Conquistadores lived, further excavations here might cast light on early historic as well as late prehistoric events. Certainly this association of early European and late Indian ceramics links the prehistoric and the early historic periods in Honduras. We also cross-sectioned mound 19, which is located about 30 meters east of mound 17 but beyond the edge of the map. This mound was about 1 meter high and 15 meters in diameter. It contained sherds and snail shells to a depth of 35 centimeters but no structural features of any sort. Here, as elsewhere in the vicinity of Naco, the underlying soil is hard and gravelly, making excavations below or beyond the artificially built or accumulated earth structures extremely difficult.

There remains to be mentioned the ball court. For present purposes the general diagram (fig. 3) and the photographs (pl. 2, fig. 1, and Strong, 1936, fig. 69) show the main features. Excavations here

were confined to the southeastern end, owing to the presence in the other end of modern burials placed here under the impression that the structure was a colonial church. The discovery of a portion of one of the ball court rings in the center of the north wall was of especial interest (pl. 2, fig. 1). A complete ring of very similar type, said to have been found at Naco by Sr. Roque Hernandez of San Pedro Sula and presented by him to Mrs. Dorothy H. Popenoe, is now at Lancetilla. It is possible that this specimen came from one of the neighboring pueblos, since none of the present Naco inhabitants remember its discovery and removal. As with the other structures at Naco, the ball court will be described in more detail at a later time.

We searched in vain for any large refuse heaps along the Naco River. Scattered sherds occur where the deeply worn trail leads down the steep gravelly bank to the river at the village but we found no thick deposits. The children brought us various fragmentary artifacts from along these banks but could show us no concentrated deposits. We saw little at Naco indicating any great antiquity, but our impressions were based on only limited study. Naco appears as a one-culture site, and we obtained no indication of stratigraphic changes.

Artifacts do not appear to be very abundant at Naco, although considerable broken pottery occurs in the various mounds and scattered along the river bank. The bulk of the ceramic remains here as elsewhere in the Ulua region are from monochrome cooking vessels which, so far as present knowledge goes, are rarely distinctive. From the samples preserved, this ware appears to be primarily dull red in color ranging from smoke-stained black to gray. For the most part it is fairly well polished, but a considerable portion has artificially scratched and roughened surfaces. Sizes are highly variable, but medium to small vessels seem to predominate. Rims are usually direct or slightly flaring; broad strap handles, notched flanges (pl. 3, *n*) and projecting lugs occur; and bottoms are either flat or slightly dimpled. Plain ware legs do not occur in our sample. The tempering of all the Naco wares is a fine micaceous grit. Particularly significant, though much less abundant, is the Naco painted ware (pl. 3). Characteristically, this ware has a white slip and painted, geometric or curvilinear decorations on both sides in red and black. One sherd (pl. 3, *a*) of this ware is unusual in showing a portion of what appears to be a plumed figure. The painted vessels appear to have been small and flat-bottomed with either direct or slightly flaring rims. Tripod supports containing rattles are very common in Naco painted ware (pl. 3, *s-w*). A strange, four-pointed,

bird- or animal-head foot is most the common type (pl. 3, *t, u*). The painted ware is not very well made, and the designs are usually badly eroded. A small proportion of unpainted and a few painted sherds have either heavily incised or raised geometric designs (pl. 4, *q, s-v, x-z*) in the interior. These were apparently made by some sort of a stamp. In one case the raised design left by the stamp was smoothed down and its outer border carved for emphasis. Three plain sherds show finely woven textile designs impressed on their inner surface (pl. 4, *n-p*). Sherds with incised designs also occur (pl. 4, *r*). On the whole, Naco ceramics consist of these two wares, the plain and the painted, but in excavations at mound I, two intrusive types occurred. The first of these, consisting of two fragments of European crockery (pl. 4, *m*), has already been mentioned. The second type consisted of three sherds of well-made, highly polished and painted ware which apparently belong to prehistoric ceramic series from other earlier sites on the Chamelecon and Ulua Rivers.

Incensario fragments from Naco are of the usual frying pan shape (pl. 4, *a*) with the distinctive Naco painted designs. Two candelarios (pl. 4, *w*) are crude but unique. They are made of unslipped coarse pottery and have tripod supports. They represent the only type found by us at Naco. Spindle whorls are quite common at Naco and are well decorated with incised designs similar to those painted on pottery (pl. 4, *i, j*). Undecorated "bobbins", probably to hold cotton thread, are even more common (pl. 4, *l*). The occurrence of spindle whorls, bobbins and textile-marked pottery bears witness to the importance of cloth manufacture in aboriginal Naco. No distinctive type of figurine was noted at Naco. The various pottery heads, ranging from simple to complex, and the "speak no evil" monkey, are illustrated (pl. 4, *b-f*). Whistles seem rare at this site. Only one specimen was found (pl. 4, *h*) and this animal form suggests Chiriqui, although the red and black paint design is in the Naco style. The only other artifacts noted were the ubiquitous obsidian prismatic flake knives (pl. 4, *k*), and fragmentary legged metates and manos of lava. At Naco, as elsewhere in Honduras, there appears to have been an amazing emphasis on pottery in comparison with any other type of non-perishable artifact. Textiles and wooden implements have left only indirect evidences of their probable importance.

LAS VEGAS

This site, also known locally as "Potrerito de los Calpullis", is located less than 1 kilometer in a direct line and about 2 kilometers by trail from Manacal (see map, fig. 2). It is a neatly arranged

mound group and is one of the few in the Ulua-Chamelecon region that can be photographed to advantage (see Strong, 1937, fig. 70). The main features are four large mounds forming a rough square, with another low mound in the center. The largest mound, to the north, is about 2 meters in height, 27 meters in length, and 12 meters in width. The others are slightly smaller, those to the east and south being rounded rather than rectangular. The eastern mound had a trench, made by workmen from Manacal, in the east side. The central mound is about 1 meter in height with a diameter of 8 meters. It is connected with the eastern mound by a low neck. The four main mounds roughly correspond with the cardinal points, but there is no exact orientation. A low, stone-covered mound is located about 40 meters to the west. The entire group is located on an open strip of high, flat land, flanked on the east by a deep gully and on the south and west by the steep river banks. An artificial terrace of river boulders borders the site to the south. Behind the site rise rolling pine-covered hills, and between it and the river proper is a densely wooded flood plain.

No artifacts occur on the surface other than a very few sherds of plain brown ware. A rounded boulder in the central plaza suggested an ape's head somewhat similar to that shown in plate 16, figure 3, but we were unable to determine whether the stone had been actually worked. The men who had dug the deep trench in the eastern mound encountered nothing but stones and broken pottery. Pottery is visible in the cut to a depth of 2.5 meters. We ran a trench through the heart of the low central mound reaching a depth of $1\frac{1}{2}$ meters in the center. The upper meter consisted of soil with many large boulders, stones, and a few pieces of plaster; below this was hard gravel. A few lava metate and mano fragments and a considerable amount of plain, brown pot sherds came from the upper meter. The Las Vegas ceramic remains are predominantly of an unslipped brown ware indistinguishable from cooking ware at Naco and in Ulua Polychrome sites. However, a few polished and slipped sherds occur, and some of these have linear designs in red and black. A few sherds of dull orange ware with red stripes, a small orange rim with red and black monkeys, and a hollow round tripod leg were also found.

TRES PIEDRAS

According to our workmen, this site received its modern name "because it is a place where they catch many fish", a puzzling explanation unless one is aware that the name "Tres Piedras" may be given to any person or place of particular potency. In a sense

Tres Piedras is a very miniature Copan since the Chamelecon River has nicely cross-sectioned it (pl. 2, fig. 4). It is located less than a kilometer down stream from Las Vegas and on the same or western bank (map, fig. 2).

Originally, the site must have resembled Las Vegas in outward appearance, having four mounds enclosing a central plaza. In the photograph (pl. 2, fig. 4) two of these mounds can be seen in cross-section on the right and left of the cut; the rear mound is visible to the left of the figures, but the fourth or nearest mound has been completely washed away except for the many boulders deposited in the river channel. A fifth mound, likewise cross-sectioned, occurs to the west. Unlike Las Vegas, the plaza at Tres Piedras had a series of three plaster floors, the highest at a depth of 1.5 meters below the present surface, the lowest at a depth of 2 meters. The material was a thick, white "mezcla" or plaster. The upper floor appeared to be flat, but the two lower floors each had one step rising to the east. From our limited excavations it was impossible to tell how extensive these floors originally may have been. Along the river bank they extended for about 10 meters, and a considerable amount of broken plaster was visible elsewhere on this general level and in the talus deposit at the foot of the bank. It seems probable that the entire court or plaza between the mounds was once paved, but until adequate excavations are made here this cannot be proved, nor can the nature of the steps or mound approaches be determined. Over the plaster to a depth of three-fourths of a meter is a thick deposit of large river boulders. These may have rolled down from the mounds or may have been placed here later to raise the level.

Among the vast quantity of stones deposited in the river bed from the portion of the site that has been washed away are many that indicate human workmanship. The most tantalizing of these are a considerable number of large lava blocks that strongly suggest sculpture in the round. None, however, are definite enough for certainty, but they do give an impression of either a dying or a nascent sculptural drive. The "ape's head" from Las Vegas is of this type and may have been transported there from Tres Piedras. In addition, there are numerous squared blocks of limestone or gray-green schist, one circular block with abrupt edges, and several thick slabs with holes drilled through them. Metate and mano fragments, as well as lapstones without legs, occur. Stones are particularly concentrated in the river bed below what was once the position of the east mound. With them occur large fragments of plaster flooring. This flooring often contains boulders or shows the molds from which

boulders came. Structurally, the Tres Piedras site appears to have been more pretentious than the majority of sites in the vicinity, and the remaining half is well worthy of complete excavation.

We made two small stratigraphic cuts, the first west of the central mound group between that and the outlying mounds to the west. The second was in the heart of the plaza. Both sections were on the face of the river bank and each was 5 meters long by 1 meter broad, extending down to sterile soil. The first excavation yielded some pottery at 10 centimeters and reached barren soil at about 1.70 meters. The second cut passed through three plaster floors and reached barren soil at 2 meters. The first yielded the most potsherds although even here they were not overly abundant. Gray to red cooking ware was most abundant in each of the five 30-centimeter levels. A very few sherds of Mayoid polychrome occurred in all but the bottom level. Above 1 meter all fragments of this type were from pots with buff to orange slips covered with florid, conventionalized, red, purplish, and black designs. Below 1 meter the same Mayoid types occurred, but in association with more realistic designs having human head panels. At this same level occurred fragments of an excellent Mayoid vessel with a panel of square, grotesque heads around the rim and, below this, an intricately carved design. The design had been carved after firing. Associated with these lower Mayoid types were a few sherds suggesting orange over buff negative painting; and cooking ware with dull, dark red line decoration. The second excavation in the plaza yielded few but similar pot sherds. However, the occurrence of a small, restorable imitation Ulua marble bowl just above the upper floor at a depth of $1\frac{1}{2}$ meters was significant. Maya carved ware occurred at this same depth in the first excavation. The three plaster floors in this second excavation have already been mentioned.

OTHER SITES

There are numerous mounds and other archeological sites in this region, but time to examine many of them was lacking. Close to Manacal Ranch is the site of Los Cocos, consisting of a few low earth and stone mounds that are being rapidly eaten away by the river (map, fig. 2). There is a deep 30-foot bank at this place. No notable structural details could be observed. The only pottery we obtained were some coarse, blackish brown sherds and one heavy, dull orange, sherd with eroded red and black designs.

Farther upstream, beyond the mouth of the Naco River, is the site of San Luis (see map, fig. 2). Here in a cut of some 3 meters occur many river boulders and large amounts of broken pottery. The

majority of the pottery is a coarse, brown or buff ware. There are also a number of heavy dull orange pieces with broad red stripes and some polish; as well as a polished red incised piece and a fragment of a heavy platter with coarse red and black line decoration. In the talus below this bank were two large, square cut stones of volcanic origin. A few crumbling human bones were also found in the bank and on the talus. There are no surface mounds at San Luis, but broken pottery occurs from just below the present surface to a depth of about 3 meters. No stratigraphic changes in type occur so far as our very small pottery sample is concerned, but the site merits much more careful study than we were able to give it.

As one rides past Cofradia on the way to Naco a few low mounds are visible to the south of the road just after one has crossed the Manchagualay River. We did not examine these in detail. Farther along the Naco road, about 1 kilometer from that village, there is a small Spanish colonial ruin located in dense bush about 20 meters north of the road. It is the foundation of a small house made of bricks and plaster, and the local people have tales concerning a magical cross of gold that was once found here. As already stated, the ruins of Naco extend for about 1 kilometer up the Naco River, and there are said to be numerous mounds across the river from the modern town. We visited the site of Quebrada Tostada, about two leagues upstream from Naco in a hanging valley some 400 feet above El Salto, the wild and beautiful falls of the Naco River. The main site at Quebrada Tostada includes 4 or 5 acres of pine- and thorn-covered land. Low stone and earth mounds are scattered over this area, and we found a few sherds of coarse brown pottery. Local tradition says that "the King", i. e., Olid, fled to El Salto after he was wounded. We cut our way down the steep, rough gorge to the falls but found no signs of any settlement there. Our guide, Don Santiago Nolasco, said that there were many low mounds scattered over the hills and mountain valleys in the general vicinity of Quebrada Tostada, but he knew of no nearby site comparable in size to the ruins at Naco.

There is another important site in this general vicinity which we had hoped to visit. This is the Bell Cave, which Blackeston (1910) located near the headwaters of a small stream flowing into the Chamelecon River, about 25 miles from the ruins of Naco. Blackeston obtained a considerable number of copper bells and a few other unusual artifacts at this site. We were told by Sr. Roque Hernandez of San Pedro Sula that the site was not yet exhausted. Just before we left Manacal, Sr. Juan Antonio Sarmiento of San Antonio Mahada offered to guide us to the cave which he said was near his home.

Unfortunately, we were unable to make the trip. It would be very important to learn what types of pottery, if any, occur in association with these copper bells. Spinden (1925, p. 544) has suggested that the cache formed part of a Toltec trader's outfit.

ULUA AND COMAYAGUA RIVERS

Our most extensive excavations on the Ulua proper were at Las Flores Bolsa and at Playa de los Muertos. In addition, ceramic samples were obtained at various river bank and mound sites between Naranjo Chino and the mouth of the Comayagua (see map, fig. 5). Our investigations were for the most part confined to the eastern bank of the Ulua. In a region as rich in sites as is the Ulua, it seemed better to confine our efforts to a few promising places rather than attempt too wide a survey. The depths at which cultural layers occur necessitated moving dirt on a very large scale for even a reasonable stratigraphic sample. On the Comayagua River, near Santa Rita, we made excavations similar to those at Las Flores Bolsa and at Playa de los Muertos.

LAS FLORES BOLSA

Las Flores Bolsa is located on the east bank of the Ulua River just south of the division line between the Las Flores and Naranjo Chino banana plantations. This was the farthest down-river site excavated by the expedition (see map, fig. 5). We worked here from January 20 to February 20, 1936. The site was chosen because of the fact that examination of the steep river bank from a dugout canoe revealed several human skeletons one above the other at this place. We therefore hoped for some sort of stratification. This was also the exact place where O. P. Swofford found a deformed skull with filed and inlaid teeth and with a jade bead in its mouth. This skull has been described as that of a Maya chieftain from Santa Ana (see Blom, Grosjean, and Cummins, 1933). It should be noted that the Las Flores site is actually a considerable distance downstream from Santa Ana (see map, fig. 5). In addition to fragmentary human bones there was a considerable amount of broken pottery projecting from the bank and on the small talus at the water's edge.

We made two deep stratigraphic cuts paralleling the bank and extending down to the water line. At the time of our work the almost vertical river bank was 5.25 meters in height. Excavation 1 was approximately 10 meters long by 4 meters wide. The top 2 meters was a recent sand and silt. Cultural debris, mainly broken pottery,

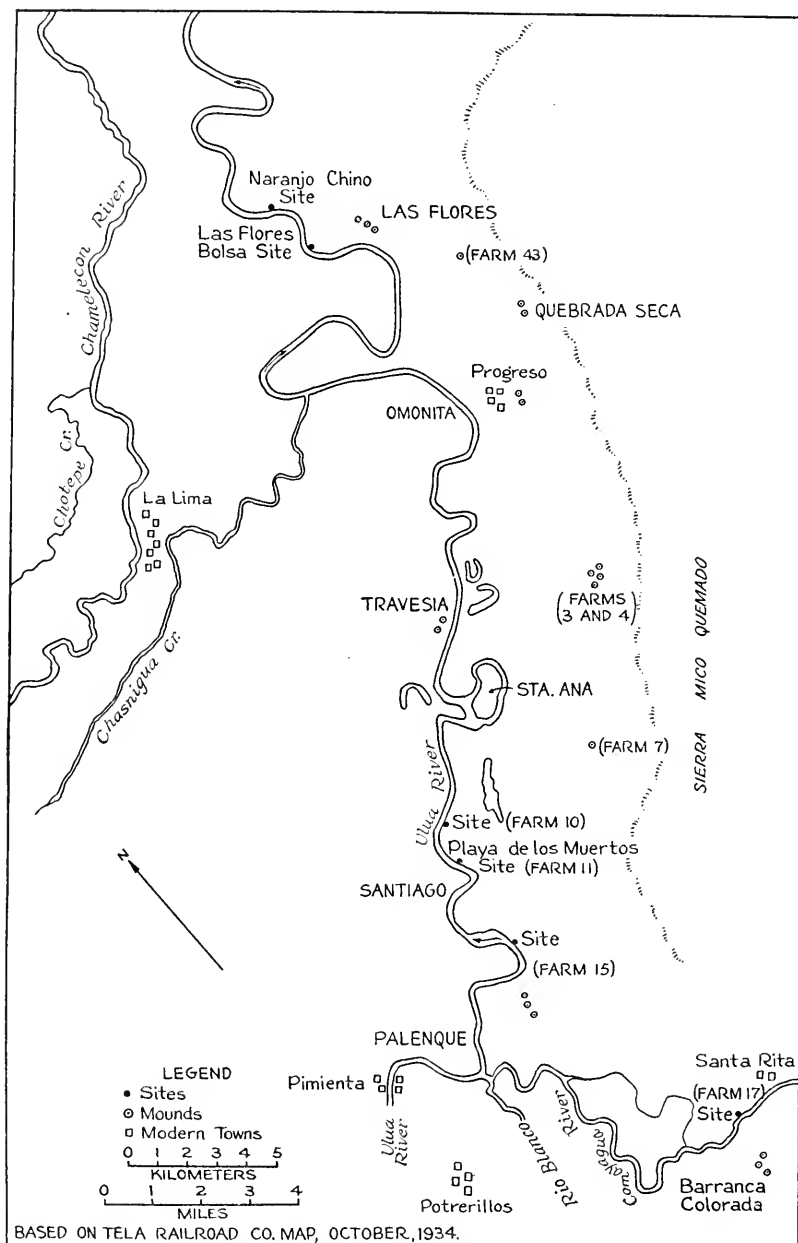


FIG. 5.—Map of the lower Ulua and Chamelecon Rivers.

occurred in the heavy clay below this for 2.25 meters; below this was a sterile light clay loam extending to and below the water level. From the point where we struck the first artifact (at a depth of 2 meters), the soil was stripped off in successive layers each 25 centimeters thick, the first one being designated as P 1 (i. e., pottery level 1) and so on through the occupation level. In all, 13 burials were encountered in this excavation, 10 extended (P 5-9) and 3 bundle burials (P 4-6). The skeletons were in crumbly condition, and the skulls were badly distorted by the pressure of the earth. Only two complete skulls could be saved. Grave gifts were sparse, no complete pots occurring with any of the burials. One bundle burial had 2 clay spindle whorls (top of P 4), and another bundle burial (P 6) had 1 copper fishhook, 16 obsidian flake knives with needle sharp points, and a broken cooking pot containing bird bones. Layers of small adobe bricks and small baked clay basins near certain burials were the main structural features encountered. Broken pottery was quite abundant in this excavation, coming from 10 levels. The types and sequence represented will be discussed in the final report.

Excavation 2 was 16 meters east of excavation 1. It was roughly 5 meters long, 4 meters wide, and 5.40 meters deep in the deepest portion. It contained only one extended skeleton (P 3). From the surface, mixed sand and silt extended down a little less than 2 meters; here the soil changed to a light clay. This layer of light clay, without artifacts, extended down slightly more than 1 meter. Beneath this was a dark, heavy clay containing artifacts. Artifacts occurred throughout 7 levels or 1.75 meters. The cultural deposit sloped down toward the south (i. e., toward the river) so that it extended to the top of P 8 there, whereas on the north side of the excavation it terminated on top of P 4. A living level occurred in P 3 and it is the termination of this which sloped down to P 8 on the river side suggesting a refuse heap. In absolute level, P 1 in excavation 2 corresponds to P 4 in excavation 1. Obviously, the deposition of refuse at this site had been little disturbed by burials. On the other hand, the occurrence of only three levels on the north side with what appears to be a dump heap (correlated with level P 3) on the south suggests that the deposit represented a relatively uniform period of no very great duration. A bed of coarse sand occurred at a depth of 4.25 meters and below this was a light clay loam extending to and below the water level. Except for the sloping dump on the south edge, this stratum was devoid of artifacts.

The various ceramic and artifact types from excavation 2 will be briefly discussed and any obvious stratigraphic changes noted.

Pottery predominates tremendously over any other form of artifact, and plain or domestic wares are much more abundant than decorated wares. In all layers at this site the pottery shows the effects of water action, and the surfaces of many sherds are eroded. There is, however, no observable indication of re-deposition. The majority of sherds from all levels are of unslipped, undecorated wares ranging in color from a smoked or burned black, through brick red or brown to light buff. Sizes are highly variable. Pots with constricted and medium flaring lips are common, as are direct rimmed bowls. Vertical strap and solid round handles are most abundant. Many of these, from all levels, have a knob, filleting, or a crude monkey head on the bend. Bottoms are flat, rounded, dimpled, and annular, the first three types being most abundant. A few plain, hollow, conical feet occur. In P 6 and 7, large, thick, highly polished sherds also occur. Since grit tempering seems practically universal in the Ulua-Yojoa region, it may be taken for granted unless variants are mentioned. Domestic (that is coarse or household) ware with painted decoration is rare at this site. It occurs sparsely in P 3 and 4 where large vessels with high flaring necks are decorated with rayed circles, cross-hatches, or lines of dull red or brown paint applied in a splotchy fashion. Plain incised ware is rare but occurs in P 4 and 5 where necks are decorated with delicate, wavy, comblike patterns forming both vertical and horizontal patterns.

With the wares which are both painted and incised we pass out of the strictly utilitarian class and find several intergrading types. A striking Las Flores type occurs in levels P 3-5 (pl. 5, *a, b, c, d, e*). These sherds are from thick-walled, vertical vases or bowls with high vertical necks, having a polished red slip, a band of black geometric designs below the lip and another band of incised design below this (compare Strong, 1935, pl. 18, fig. 1, *b, c, e*, for similar Bay Island types). Another striking and distinctive ware, which occurs commonly at Santa Rita (farm 17) (pl. 7, *a-d*) and rarely at Lake Yojoa (pl. 14, *d*), we have here called the Bold Geometric, monkey-handled type. It is very similar if not identical with Bay Island Polychrome II ware figured elsewhere (Strong, 1935, fig. 11). This is found in all levels at excavation 2 but undergoes some change in the two bottom levels. The typical vessel is large, with an orange slip and intricate black and red geometric designs around the neck, the body, and on the handles. The neck design is often of the interlocking textile type (compare pl. 5, *c*, and Strong, 1934a, fig. 54, and 1935, fig. 11), and the handle at the bend usually has a monkey head in relief with modeled or punctate features. At Las Flores, excavation 2, numerous

sherds of this type have incised as well as painted designs around the neck. The more or less realistic birds and animals occurring on vessels of this type from the lower levels at Santa Rita (farm 17) (pl. 7, *b-d*) are lacking at Las Flores. In levels P 6-7, vessels of this type have lower necks, irregular handles, and incised as well as painted designs.

Polychrome sherds from thin-walled, vertical vases of so-called Mayoid type occur in all levels in excavation 2. The majority have florid, conventionalized, all-over designs in red, black, white or purple on buff, orange, black, or white slips (pl. 5, *f, g, h, i, j, k, l, m*).

The majority of designs are elaborated and extremely conventionalized reptilian, animal, mask, or anthropomorphic forms. They often cover the entire surface of the vessel and are difficult or impossible to reconstruct in their entirety from sherds. Crude skeuomorphic glyph bands occur from P 5-7, as do elaborately modeled projecting monkey or animal head lugs in the same levels (pl. 5, *f, g*). In some cases the designs are outlined with incisions. In the upper levels several sherds with red and purple spots occur (pl. 5, *j*). Bases are flat, dimpled or annular, and hollow cylindrical as well as solid, thin, rectangular, tripod legs occur in all levels. None of the isolated and graceful processional or "dancing" figures occur in excavation 2, although a few sherds with this type of decoration were found in the deepest levels of excavation 1.

In addition to polychrome, straight-walled vases, a number of low bowls or small jars have similar types of designs. In P 1-2 occur polished red or orange sherds. In P 3 there are fragments of about six small jars with solid rectangular, tripod feet and eroded black and red designs. From P 4 to P 7, small tripod jars and low bowls with an orange slip, and red and black conventional or crudely realistic designs are common. These are in the Mayoid rather than the Bold Geometric tradition, though an occasional blending between these major styles occurs. In some instances incision is used to outline painted designs. In P 7 was found an unusual, restorable bowl of thin, polished ware, with an orange slip, and conventional, black and red, monkey and rosette designs outlined with incisions, a dimple base, and a low "vestigial" spout to one side of the direct rim (pl. 6, *b*). Three similar low "vestigial" spouts occurred in P 2-3 as well; hence they cannot be regarded as strictly early at Las Flores.

From P 5-7 came a few fragments of Mayoid sculptured pottery. A restorable tripod vessel of this type is painted all over with an orange wash, except for the carved panel of elaborate Mayoid faces which apparently had no slip (pl. 6, *d*). A tiny vessel with a similar

face panel is brown with no slip. It has an annular base and in shape rather suggests certain of the Ulua marble bowl types, though the sculptured design is Mayoid. A third fragment is the rounded bottom of a bowl with intricate Mayoid design in high but rounded relief. The slip was originally red but has disappeared except between the raised designs, and glittering micaceous tempering material shows on the surface. If it were not for Lothrop's statement (1936a, p. 142) that this mold-made appearance is due to delicate carving and the obscuring effect of the slip, one would be inclined to regard these as stamped or molded rather than carved. The type will repay much more detailed analysis than is possible here. From P 5 and 6 come three small restorable pots of the imitation Ulua marble bowl type (pl. 6, *e*, *f*). There are a few other sherds of this type. No slip is visible on these pieces, though all are considerably eroded. The association of Mayoid sculptured ware and imitation Ulua marble bowl pieces in the same levels may very well be significant.

Incensario fragments occur in every level except P 1 and P 7. All seem to be of the usual perforated frying pan type with hollow, round handles. They lack painted decoration and range from light buff to brown in color. Fragments from P 2 and P 6 are very thin and delicate, but a fragment from P 3 is thick and crude. Candelarios, or small incense burners, occur in P 3 and P 5. All are of the unslipped, single-hole type. That from P 3 is undecorated, whereas the two fragments from P 5 have crude linear incision and punctate ornamentation. Cassava-grinders, or round, handled, disks of coarse pottery, with one surface ridged with cross-hatched incisions like a grater, occur from P 3 to P 6. They are most numerous in P 3. Spindle whorls occurred only once, with burial A 1 in level P 4. Of the three, two were plain and one had neatly incised decorations.

Figurines and whistles occur in practically all levels. They show little change in types from top to bottom. Solid, mold-made figurines of Mayoid type (like fig. 7, *s*) occur in P 2, 5, and 6. A portion of a pottery figurine mold was found in P 5. Modeled figures of thin, polished, brown pottery occur from P 2 to P 7. Some of these were originally rather pretentious (pl. 6, *a*), but nearly all are very fragmentary and their original form often cannot be determined. Besides the human figurines and larger hollow statues, both solid and hollow animal and bird heads occur in all levels. Many of these were probably from whistles (like fig. 7, *a*, *c*, *e*). Similarly, many of the human figures once formed parts of whistles. Strange bulbous animal forms occur from P 2 to P 7. Some of these were whistles, others were not. A particularly interesting whistle from P 2 is in the form of a realistic

frog with a small one on its back (compare Gordon, 1898, pl. 9, *i, j*). Pottery stamps likewise occur from top to bottom. From P 1 comes a round, stemmed stamp with a neat monkey design; from P 5 a rectangular, stemmed stamp with a squirrel design and a butterfly-shaped stamp with two crude faces; from P 6 an elaborate froglike stamp with small circles for designs, and, from P 7 a rectangular stamp with a geometric design.

Compared to the amount of pottery recovered from this excavation, the total list of other artifacts is pitifully small. P 1 yielded 1 broken T-shaped drill of obsidian; P 2, 30 fragments of obsidian flake knives, 1 crude obsidian drill, 2 polished pebbles, 1 piece of crudely flaked quartzite; P 3, 2 crudely chipped stones, 1 polished pebble, 2 pieces of baked clay with wattle and daub impressions; P 4, 1 lump of clay; P 5, 6 fragments of obsidian knives; P 6, 1 obsidian knife fragment; 2 quartzite stones, 1 smoothed piece of baked clay, 1 large alligator (?) bone with 2 perforations, 1 tapering, cylindrical brick of baked clay; and P 7, the butt end of a small celt of hard green stone. This slim list clearly indicates what a tremendous proportion of the ancient material culture was perishable. Were it not for the advanced and abundant ceramic remains in prehistoric Ulua sites, one might reasonably, but erroneously, conclude that only a very simple prehistoric culture had flourished there.

SANTA RITA (FARM 17)

Excavation work was carried on at this site by Dr. and Mrs. Kidder from the middle of March until the rising water level drove them out of the excavations on May 20, 1936. Work was also going on at Lake Yojoa, but all the other members of the expedition spent some time in the Santa Rita excavations. The site is located on the Comayagua River just below the little town of Santa Rita (map, fig. 5). It consists of refuse deposits and living levels exposed in the steep banks of a flood channel of the river and is only 200 meters west of the overseer's house on farm 17 of the Tela Railroad Co. The main irrigation canal for the lower valley takes out from the Comayagua just east of the overseer's house. Thanks to the courtesy of the Tela Railroad Co. and of the overseer, Mr. John Thompson, we were able to board comfortably at the farm house and to use its broad porches for sorting specimens.

The physiographic and cultural evidences revealed by the Santa Rita excavations are complex and require far more detailed treatment than is possible here. However, certain very significant correlations

between these factors are already apparent, and these can be briefly outlined. In all, three adjoining excavations were made at this site, the main stratigraphic cut designated as excavation 1; a northern extension of this cut resulting from the discovery toward the close of the work of older and deeper cultural material; and excavation 2 extending through a polychrome refuse heap to the east. For present purposes we will confine our remarks to excavation 1 and, to a lesser extent, to the northern extension. The beginnings of all these cuts can be seen in the illustration (pl. 2, fig. 3).

A cross-section (fig. 6) of the west end of excavation 1 shows the outstanding stratigraphic features. This excavation was originally 5 meters long from east to west, paralleling the cut river bank, and 4.5 meters in width from north to south. Owing to the outward slope of the bank, the bottom of the excavation was 8 meters in breadth (fig. 6). When the May floods made further work impossible, we had reached a depth of 5.20 meters in excavation 1 and 5.40 meters in the northern extension. In size, the northern extension was less than one-third of excavation 1.

The cross-section along the west wall of excavation 1 (fig. 6) shows the various soil layers. The 2 upper meters consist of alternating deposits of dark silt, light silt, and sand. Below this is a thick deposit of dense clay which terminates at a total depth of 3.80 meters in a thin bed of sand or sandy silt (level 8, fig. 6). This sand layer has here a slight dip from the north and thins out near the southern edge. Beneath this layer is a sandy clay (level 9, fig. 6) which, with certain minor changes, extends down to the bottom of our excavation. On the extreme southern edge and in the deepest portion is a deposit of sand and gravel (fig. 6) which ran the length of the excavation and may represent an old stream bed. In the west wall cross-section the sand layer (level 8, fig. 6) seems to dip toward this sand and gravel deposit but, on the east wall cross-section, the sand is much thicker (40 cm) and extends on a level plane to the edge of the bank at a point 1 meter above the lower sand and gravel deposit.

The first potsherds and other cultural detritus occur in the dense clay deposit simultaneously with a layer of river boulders (fig. 6). Throughout this clay deposit polychrome pottery is abundant, as are other cultural manifestations. The polychrome debris is thickest in a definite refuse deposit on the southern edge which dips slightly less than 1 meter below the main clay and pottery-bearing stratum (refuse heap, fig. 6). Debris extends down almost to the low sand and gravel deposit suggesting that it had been dumped over a low bank at the edge of an old water course. The refuse heap here

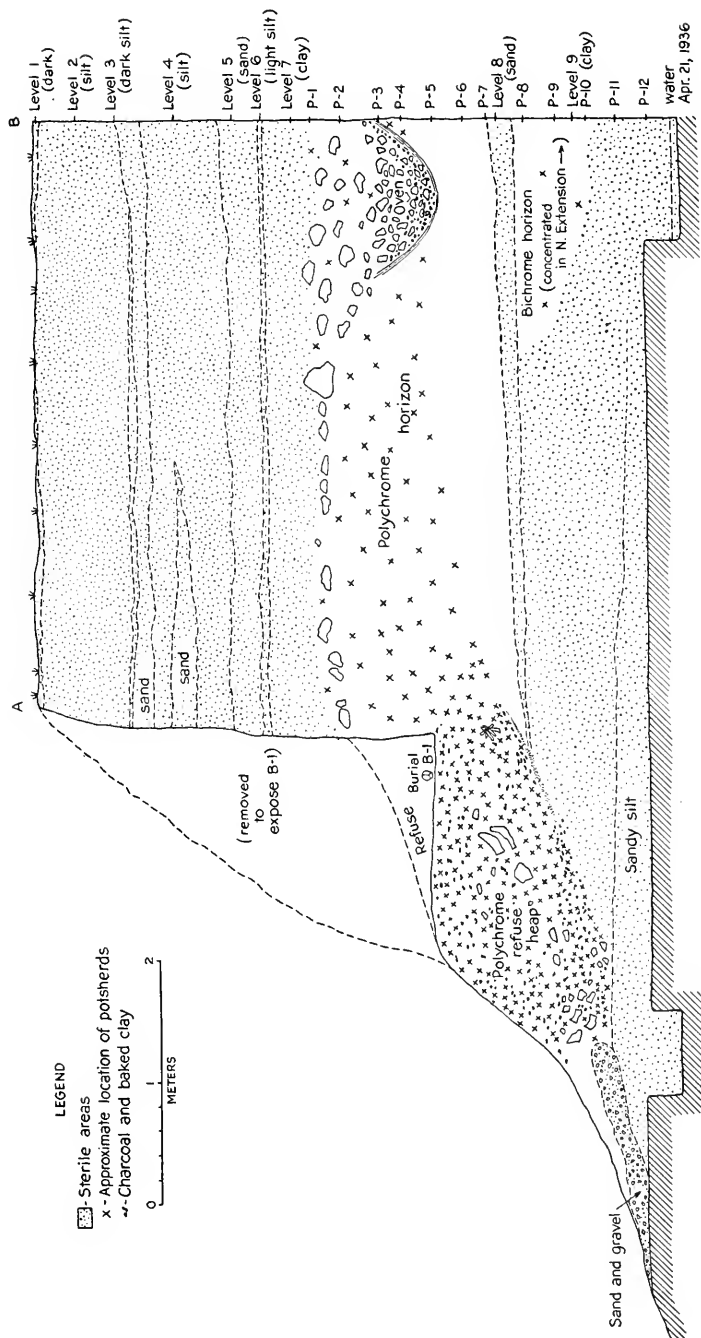


FIG. 6.—West wall of excavation I, Santa Rita (farm 17).

terminates before the east wall of excavation 1 is reached, but beyond this point another polychrome refuse heap at the same depth occurs and it was in this that we made excavation 2. The sand level (level 8, fig. 6) was sterile of artifacts throughout all of our excavations. In excavation 1, the same was true of the underlying sandy clay (level 9) except on the southern edge where the overlying polychrome refuse material dipped, and at the northern edge where a very few monochrome potsherds were encountered (level 9, fig. 6). These latter, found toward the end of our work, seemed highly significant and for this reason the northern extension was made extending north from the northwest corner of excavation 1. Soil layers and pottery deposits were generally similar in excavation 1 and in the northern extension. However, in the northern extension more abundant potsherds differing from the polychrome type were found in the sandy clay (level 9, fig. 6) beneath the sterile sand stratum (level 8). This will be discussed subsequently.

Cultural features, other than abundant potsherds and rare artifacts, were not marked in any of the excavations. River boulders occurred throughout the upper portions of the main clay stratum (level 7, fig. 6) in all. What appears to have been a roasting pit or oven is outlined in figure 6. Small clay-lined fire pits and small irregular clay bricks also occurred. Eight burials, all in bad condition, were encountered, four in excavation 1 and four in the northern extension. In all cases these occurred either in the clay stratum (level 1) containing polychrome pottery or just below it and clearly intrusive into the sand. All were extremely friable and crumbled on exposure to the air. One of the burials in excavation 1 was extended and had notched upper incisors, three were flexed, only one had any grave gift (a ground stone knife). In the northern extension, one burial consisted merely of an immature skull, jaw, and humerus; one was extended; one was flexed; and the last was the extended skeleton of a new-born child under a large, plain red, two-handled bowl. Excavation 2 yielded no burials.

The succession of ceramic and artifact types from excavation 1 and the northern extension will be briefly outlined. This site was richer in polychrome pottery than any other we dug on the Ulua, but it should be remembered that even here there was much more plain than painted ware. The sherds from this site show little erosion through direct water action and the majority of the painted pieces are fresh and bright. We will discuss the material according to four major stratigraphic levels, A (P 1-3, see fig. 6), B (P 4-6), C (P 7-9), and D (P 10-12). As indicated on the diagram (fig. 6) levels

A include the upper portion of the clay occupation stratum. The southern face of the cut, including the uppermost portion of the refuse heap, had been removed to expose skeleton B 1 prior to completing the diagram. Levels B include the lower portion of the clay occupation level and the upper portion of the southern dump heap. Levels C, the very bottom of the clay occupation level and the middle of the dump heap. Levels D include the lowest portion of the dump. With the exception of this southern polychrome dump heap, most of the remainder of levels C, and all of levels D, were devoid of artifacts except in the extreme northern portion where a very few bichrome sherds were encountered beneath the sand stratum (level 8, fig. 6). These will be discussed separately.

Levels A contained a large amount of plain cooking ware of a red brown to blackish gray color. The vessels were fairly large, including direct bowls and pots with flaring necks and vertical handles. These handles are either round or flat in cross-section and, in a few cases, have a monkey head lug on the bend. Rounded, flat and dimpled bases and a few conical and round hollow feet occur. There are also some highly polished thin sherds tan or buff in color. The upper portion of B contained the same types but in the lower portions crudely painted ware superseded the plain cooking ware. In C and D plain cooking ware was very scarce except for a few very thick gray and brown sherds and some vertical strap handles. A portion of a thick, plain tray with horizontal handles occurs in C, and a plain annular base in D. Similar cooking ware but decorated with blotchy red or brown designs on neck and body occurs in A. These designs are usually rayed circles, criss-cross lines, and more or less irregular blotches. In B this type supersedes the plain ware in the lower levels. A squat, swollen pot form with flaring neck and vertical handles is characteristic. These are better made than in A, and the dull red, criss-cross line decoration on a lighter background sometimes suggests negative painting. This type also predominates in both C and D where undecorated domestic wares are rare. Plain incised ware is lacking in all levels. From both A and B levels came a few similar pot fragments in which the neck of the vessel is also incised with delicate, wavy, vertical lines and where the handle is replaced by small tripartite adornos. This variant of the swollen, simply-painted pot is more numerous in the lower levels, i. e., C and D. In D there is some blending of this type with the Bold Geometric, monkey-handled ware. Three sherds from thick-walled, vertical vases have a slip and painted designs with a band of heavily incised decoration around the upper

body. They all come from A and closely resemble the more numerous representatives of the type from Las Flores Bolsa (pl. 5, *a-e*).

The Bold Geometric polychrome type occurs in all of the lower major levels at farm 17. In A it occurs only in the lower third (i. e., level P 3, fig. 6). The vessels of the characteristic swollen olla type are medium rather than large in size. Textile and geometric designs are common (figs. 8, 9, compare Strong, 1934a, fig. 54, p. 46), but conventional birds and animals are lacking. In B similar designs occur in the upper two-thirds, and a few animal and bird designs occur in the lower third. In C and D animalistic designs (pl. 7, *b-d*, and fig. 10) are common, but geometric and numerous textile motifs also occur. The Bold Geometric vessels of the lower levels appear to have been slightly larger and better finished than those from the upper levels. Characteristic cursive, conventionalized bird, feline, bat, and reptile designs from the lower levels are illustrated (pl. 7, *b-d*, and fig. 10) and their association with geometric motifs indicated. In D a few Bold Geometric type vessels have incised patterns on the neck, similar to the squat, painted and incised domestic ware previously described. Bold Geometric monkey-handled bowls are numerous at this site and, with the straight-walled Mayoid vases, constitute one of the two most distinctive ceramic types.

Straight-walled, vertical vases of Mayoid type are represented by sherds from all four major levels in excavation 1. In A the predominant, painted decorations are complex over-all designs on white, black, orange, or yellow backgrounds. Designs are in red, black, white, purple, and, in one case, blue.

As at Las Flores Bolsa (pl. 5, *f-m*), the majority of the design motifs from A are elaborately conventionalized monster animal or human forms. One large fragment has a conventionalized jaguar with a row of conventionalized human heads above. An elaborately modeled and painted monkey-head lug occurs, as do hollow cylindrical feet and two annular bases. In B similar types occur, with the addition of textile designs and the common occurrence of bands of conventionalized heads of several types (compare upper panel, pl. 8, *a, b*, and fig. 13). Squat, elaborated human or deity figures (pl. 8, *d*, and fig. 13) occur in this horizon and one of these is outlined with carved lines. An elaborate modeled monkey-head lug and a black monkey in low relief on a painted bowl came from levels B. One sherd with blue paint used as a design was noted.

In C, panels containing paired "dancing figures" occur for the first time. This unique design motif, on beautifully polished and painted pottery, has been noted from northern Honduras to Salvador.

Lehmann (1910, p. 740 and illus. 8, p. 736) believes that copulation, not dancing, is indicated by this design and supports his view by a drawing of a Salvadorean example. To us, the latter seems no more definite than do the Ulua examples here illustrated (pl. 8, *a*, *b*, and fig. 14). In the light of Palacio's information regarding the ceremonial importance of the mutilation of male genitalia among Pipil and Lenca, we rather incline to connect this widespread design with phallic rather than procreative rites. Undoubtedly, the correlation of outer dancing figures with a unique design inside such vessels (fig. 14) is significant. This peculiar, and always slightly variable, inner design suggests some sort of record. It occurs inside "dancing figure" and certain processional vases and bowls from the Ulua River, Comayagua River, and Lake Yojoa. We suspect it also occurs inside Salvadorean vessels. This is an extremely interesting problem which at this time may only be mentioned in passing. Associated with the "dancers" are sherds decorated with isolated, processional figures. Like the "dancers", these are usually well proportioned and graceful. The manner in which they are fitted into the simpler but more beautiful panels and design areas contrasts markedly with the florid, over-all designs of the upper levels. With these more realistic figures occur a variety of conventionalized human head designs (pl. 8, *a*, *b*). Similarly, the squat, conventionalized deity or priest figures (pl. 8, *d*, and fig. 13) also occur in association with the well-proportioned "dancers" and processional figures. Flat bases are most common in this level, and tripod feet are usually solid and rectangular or ovoid, though a few cylindrical feet occur. Lugs and annular bases do not occur in our sample. Levels D are identical with levels C so far as the Mayoid cylindrical vase shapes and designs are concerned. As was true of the Bold Geometric ware there is here also a slight but obvious development from the realistic to the conventional in painted decorations. It is significant, however, that during the time involved in these stylistic changes, neither the basic form of the Mayoid straight-walled vase or the Bold Geometric monkey-handled pot changed in any very marked degree.

Fragments of Mayoid sculptured ware, as well as some examples of carved designs, come from B and C. From levels C there are two fragments from small jars in imitation Ulua marble bowl style (compare pl. 6, *e*, *f*). Here, as at Las Flores, Mayoid sculptured ware and imitation Ulua marble bowl incised ware are in close association. At Las Flores, excavation 2, these are in the lowest levels; at Santa Rita, excavation 1, in the two middle levels.



FIG. 7.—Hollow figurines, whistles, and "candelario", from the Ulua Polychrome period, Santa Rita (farm 17). (Specimens in National Museum of Honduras at Tegucigalpa.)

Numerous small polychrome jars and vases are represented in excavation 1. Certain of these are Mayoid, others Bold Geometric, and still others suggest blends between the two (compare figs. 11, 12, 15). Any attempt to clearly delineate these two major Ulua polychrome styles, or to demonstrate the exact nature of their blending, would necessitate a far more extensive analysis of design motifs than is possible here. Considered very generally, however, there are certain top-to-bottom variations which seem to be significant. In A, small red bowls with black geometric designs and conventionalized animal or anthropomorphic designs, either outside or inside, occur. Some of these are definitely Mayoid in feeling, having circle, diamond, or feather designs and dimpled bottoms. The majority, however, seem more closely allied to the Bold Geometric type. In C, an orange tone is particularly prevalent and numerous pieces show a rather unique blending of Mayoid and Bold Geometric styles (compare figs. 11, 12, 15). Conventionalized birds, animals, and reptiles occur both outside and inside open bowls (compare the similar bat designs on two vessels from approximately the same levels in excavation 2, where one (fig. 15) has a Mayoid, the other (fig. 10) a Bold Geometric feeling). Both flat and dimpled bottoms occur in C. In D there are numerous small flat-bottomed jars of Mayoid type with processional figures and other elaborate anthropomorphic designs, and open bowls with Bold Geometric designs on the inside. These less clearly pronounced vessel forms, therefore, seem to recapitulate the tendency to change from realistic to geometric decoration observed elsewhere.

A few fragments of polished gray ware came from Levels A, B, and C. The fragments were from small, slightly pear-shaped bowls without legs or handles. One fragmentary vessel had a narrow band of red paint around the inside of the neck. Another interesting feature in levels C is represented by two very definite spouts of red and brown polished ware. They are more similar to those from the deep layers at Playa de los Muertos (pls. 10, 11) than to the "vestigial" spouts from Las Flores (pl. 6, *b*). Strange to say, no Plumbate ware occurred in any of our excavations.

At Santa Rita there are two other distinctive polychrome vessel types, both of which were lacking in excavation 2 at Las Flores. One of these, a flat plate on high tripod legs (pl. 8, *e, f*), may be called a tripod plate. The other, with somewhat higher walls, and either low (fig. 8) or high (compare pl. 12, *f*) tripod feet, may be termed a tripod dish. In excavation 1, tripod dish fragments are lacking in A, fairly abundant in B, still more numerous in C, but rare in D. They characteristically have more or less intricate and geometric, red and

black designs on a light red or orange back ground (fig. 8 and pl. 7, *e*). An unusual vessel of this type from excavation 2, which has loop handles and an auxiliary annular base, is also figured (fig. 9). In general, at Santa Rita, these vessels are in the Bold Geometric style, though elsewhere (as at Lake Yojoa, pl. 12, *f*) they may be more Mayoid. Tripod plate fragments or restorable pieces (pl. 8, *c*, *f*) are rare in levels A and B, fairly numerous in C, and rather abundant in D. Characteristically, the tripod legs are high with vertical slits and contain rattles. The plates are heavy and flat with slightly inward-dipping rims (pl. 8, *f*). The designs are often

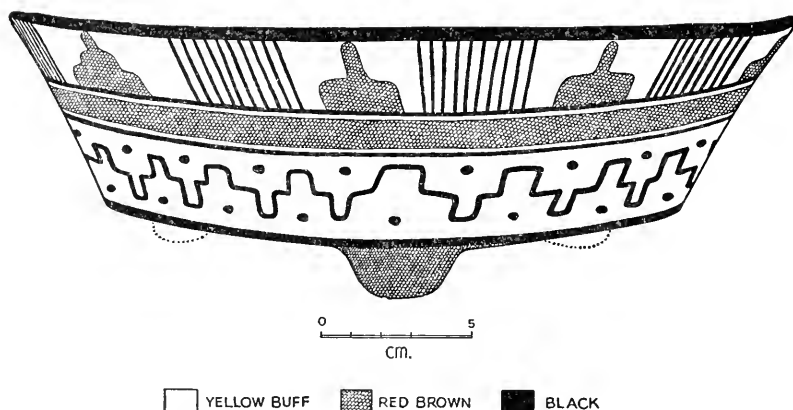


FIG. 8.—Ulu Polychrome, Bold Geometric tripod dish, excavation 2, Santa Rita (farm 17). (Specimen in National Museum of Honduras at Tegucigalpa.)

intricate, conventionalized serpents (pl. 8, *e*) in black and dark red on a lighter red background. Although very involved, such designs are often very irregular in execution. The style seems rather unique but is more "Mayoid" than Bold Geometric in feeling.

No incensario fragments came from levels A in excavation 1. From B are nine unpainted incensario fragments, all of the perforated "frying pan" type. The handles are tubular, except one that is rather crude and solid. Two handles end in clutching triangular claws and one has slits down the side. The same number of fragments came from levels C, but half are painted with dull red and brown stripes or simple geometric polychrome designs. Two fragments came from D, one plain handle has a horizontal slit and another is painted with red and black. There is some indication here that painted incensarios may be relatively earlier than unpainted ones.

Candelarios are lacking in levels A. In B two were recovered, one decorated by an incised bird (compare fig. 7, *j*) and one with incised lines. Both are of the single-hole variety. Levels C yielded one two-hole candelario decorated with a delicate incised pattern. Six candelario fragments came from D, one plain two-hole type and five single-hole specimens. One of the latter was decorated with a nicely executed textile design unit. There were no fragmentary cassava-grinders from levels A, but B yielded one, C five, and D seven. One of the latter is almost restorable. Like the others, it was of coarse gray pottery, round, with a broken strap handle on the rear and a series

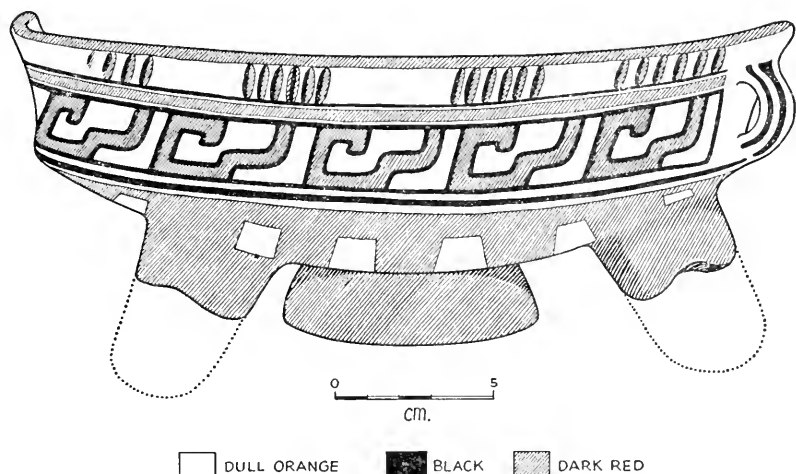


FIG. 9.—Unusual Ulua Polychrome, Bold Geometric dish, excavation 2, Santa Rita (farm 17). (Specimen in National Museum of Honduras at Tegucigalpa.)

of very rough-edged incisions or graters on the face. Only one plain, biconical, pottery spindle whorl was recovered. It came from levels D.

Figurines and whistle fragments were, rather strangely, completely lacking in levels A and D, at excavation 1, though they were fairly abundant in the two middle horizons, B and C. Excavation 2 yielded the finest assortment of such modeled pieces, and certain of these, now in the National Museum of Honduras, are reproduced here from our field sketches and photographs (fig. 7). All of these came from the polychrome horizon between pottery levels 8 and 11 in excavation 2, but, in general, are similar to the fragmentary pieces from levels B and C in excavation 1. The latter types show no obvious stratigraphic differences; fragments of large ornate busts and statues of polished brown pottery (like pl. 6, *a*); solid, mold-made figurines of Mayoid

type (like fig. 7, *s*); hollow faces with beards or ornate head dresses (like fig. 7, *m*), bulbous human, animal or composite figures (like fig. 7, *h*, *r*), tubular birds (fig. 7, *e*), howling dogs, (fig. 7, *c*), and

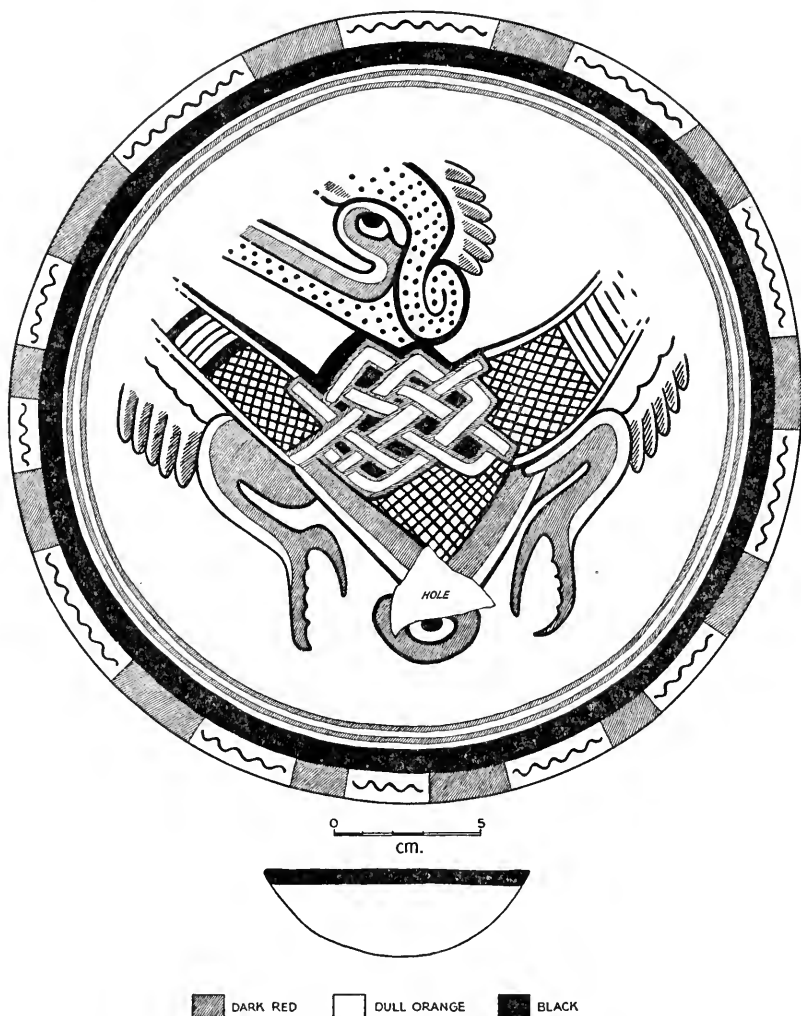


FIG. 10.—Ulua Polychrome, Bold Geometric bowl, excavation 2, Santa Rita (farm 17). (Specimen in National Museum of Honduras at Tegucigalpa.)

a variety of squatting animals (like fig. 7, *a*, *k*, *p*) all occurred in both horizons. Some of the smaller human figures were once attached to whistles, but many are simply figurines, or ornate hollow statues whose functions remain conjectural. Only a few exceptional pieces

show any traces of painted decoration. From C came a fragmentary animal with a mouthpiece suggesting a spout. An incensario or pot cover, from P 10-11 in excavation 2, representing a deer similar to certain figures in the Dresden Codex, is remarkable (pl. 8, c). At present the distribution of these numerous products of the sculptor's art gives little indication of the lines of their development within the polychrome period on the Ulua. However, comparison with similar types from earlier horizons and a complete typographical analysis will be a large and important task.

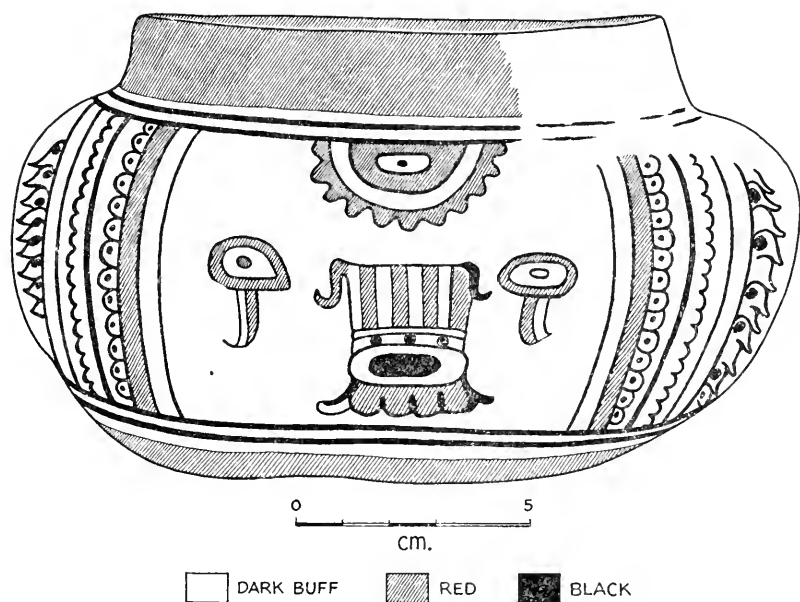


FIG. 11.—Ulua Polychrome bowl, excavation 2, Santa Rita (farm 17). (Specimen in National Museum of Honduras at Tegucigalpa.)

Pottery stamps are rare from excavation 1, though they were fairly numerous in excavation 2. In excavation 1, levels A yielded one cylindrical, roller stamp with a neat, squatting monkey design; and one flat, stemmed stamp with a geometric design. Levels B and D yielded no stamps, but levels C yielded one flat stamp with a conventionalized serpent head design.

As at Las Flores Bolsa, the disproportion between the abundant ceramic remains and all other artifact types was enormous in excavation 1, Santa Rita. Levels A produced one large, conical, stone pestle and one obsidian flake knife; levels B, six pieces of ground-

down animal rib-bones and one ground stone knife; levels C two small, polished bone needles, two obsidian flake knife fragments and one ground stone knife; and levels D yielded, aside from ceramics, nothing but one small stone celt.

Soil conditions in the northern extension were practically identical with those in the main portion of excavation 1 (compare fig. 6). The occurrence of four burials in the northern extension has already been noted. As in excavation 1, the polychrome horizon in the north-

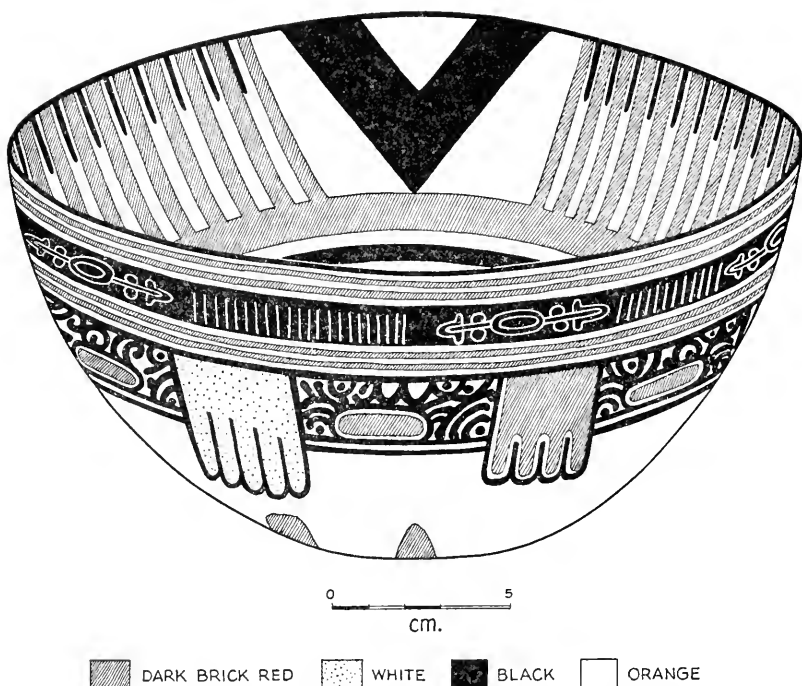
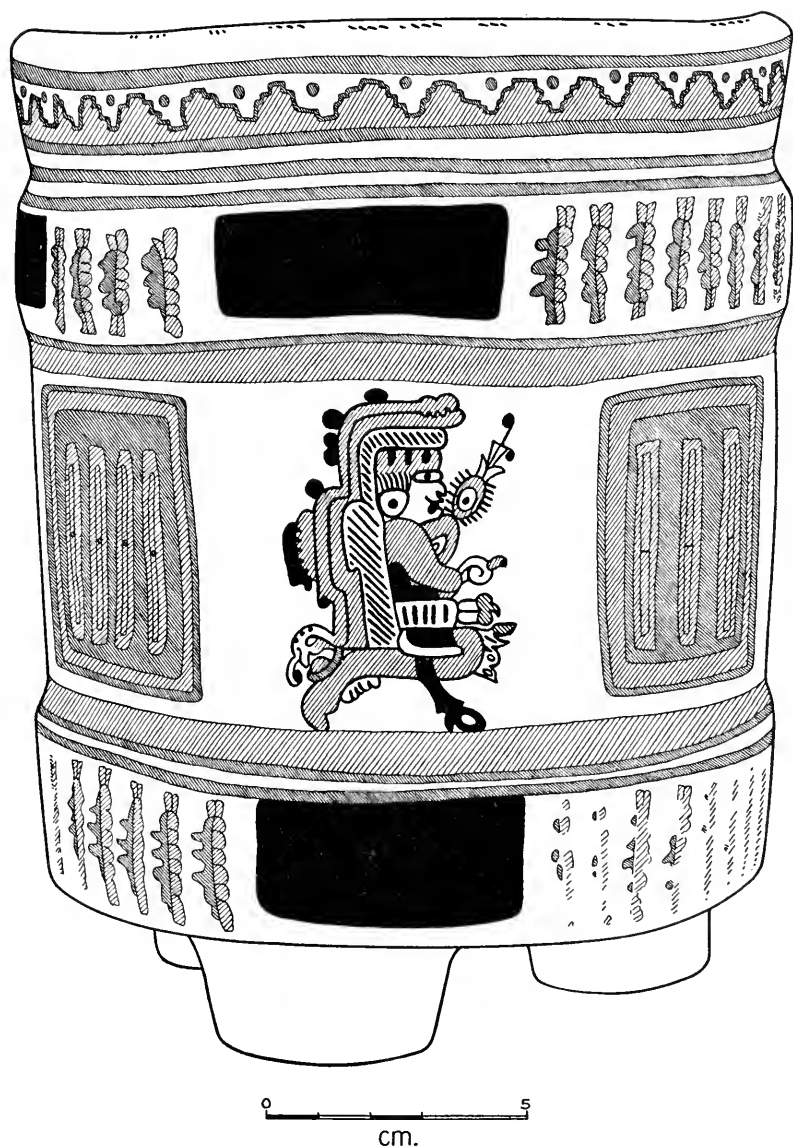


FIG. 12.—Uluá Polychrome bowl, excavation 2, Santa Rita (farm 17). (Specimen in National Museum of Honduras at Tegucigalpa.)

ern extension corresponded with the dense clay stratum (level 7, fig. 6) and was marked by a concentration of river boulders in the upper levels. In the northern extension the polychrome horizon (and burials) which were included in pottery levels A and B, terminated abruptly just above the sand layer (level 8, fig. 6). The latter was sterile and averaged 20 centimeters in thickness throughout this area. As in excavation 1 (excepting the polychrome dump heap on the southern border) the polychrome pottery horizon in excavation 2 terminated abruptly on the sterile sand stratum. However, under this



BROWNISH DARK RED
 ORANGE BUFF
 YELLOW BUFF
 BLACK

FIG. 13.—Uluja Polychrome, Mayoid vase, excavation 2, Santa Rita (farm 17).
(Specimen in National Museum of Honduras at Tegucigalpa.)

sand in C (P 7) there occurred a considerable number of potsherds of a different monochrome or bichrome type. These were in a clay stratum and were mainly concentrated in P 7, although they occurred very sparingly in D (down to P 12). Only three sherds came from P 12. This lowest clay stratum was sandier at the bottom of the excavation.

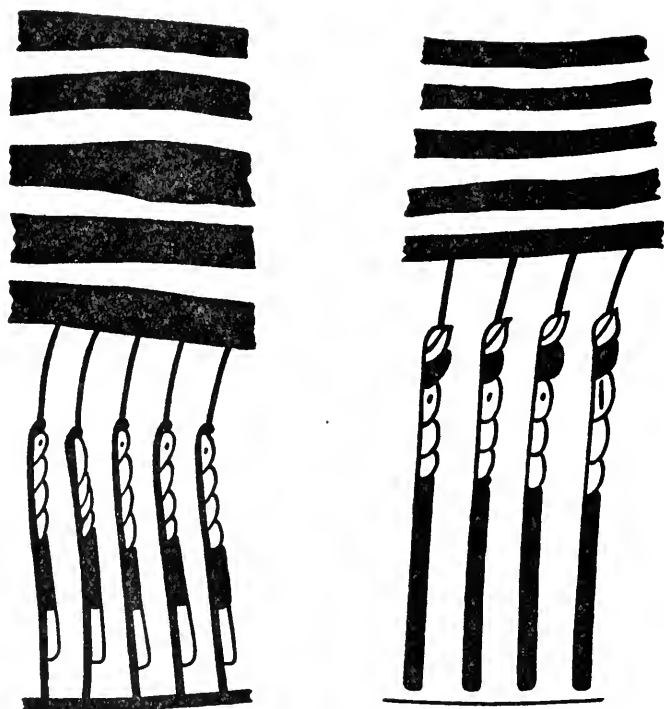


FIG. 14.—Inside design from Ulua Polychrome, Lower Mayoid vases (pl. 8 *a, b*), excavation 1, Santa Rita (farm 17).

Space permits only a very brief analysis of the ceramic sequence in the northern extension. Dividing the 12 pottery levels (P 1-12) as in the main excavation, A (P 1-3) contained considerable amounts of undecorated cooking ware; some fragments of straight-walled Mayoid vases with black slip, florid designs, and solid rectangular legs; a few small Mayoid bowl fragments; a few fragments of Bold Geometric ware; and, finally, several sherds from thick-walled, painted and incised vases (Las Flores type, pl. 5, *a-c*). B (P 4-6) contained numerous sherds from excellent, thin Mayoid vases with an orange slip and well-executed bat and thin-line human designs in

black and red (an excellent example from P 12, just above the sand, is illustrated in pl. 9, *t*). In addition, B contained a number of non-descript polychrome pieces. As in the main excavation, the lowest polychrome types in the northern extension were the best finished and had the most realistic and artistic designs. The sand level below P 12 was barren of artifacts.

Below this sand level (layer 8, fig. 6) potsherds were rather numerous in P 7 and occurred in very small quantities down to P 12 (i. e., through C and D but concentrated in the upper portion of C). All of these sherds are monochrome or bichrome and not a single example



FIG. 15.—Ulu Polychrome bowl, excavation 2, Santa Rita (farm 17).
(Specimen in National Museum of Honduras at Tegucigalpa.)

of either Mayoid or Bold Geometric polychrome occurred. The sample is too limited to define the type adequately but is undoubtedly significant as indicating a different and earlier ceramic type, here designated Ulu Bichrome, at this site. The majority of these lower sherds are monochrome ranging from highly polished red and orange ware to more numerous coarse brick red or sooty gray sherds. The highly polished red or orange sherds show examples of flat, heavily incised lips (pl. 9, *i*, *n*); swollen lips (pl. 9, *f*); flanges below the rim; flat bottoms; and small, solid tripod feet (pl. 9, *aa*, *bb*). They are from small vessels for the most part. The paste and tempering of these pieces is very fine and the ware is light and hard. A direct rim from a bowl of this type has a light gray polished interior.

A number of the orange sherds (pl. 9, *o*, *p*, *q*, *r*, *s*, *u*, *v-z*, *aa*, *bb*) are definitely of Usulután ware (Lothrop, 1933, p. 50). The faded red

or black linear designs on the bright orange background makes them very hard to distinguish from examples of negative painting since the slip at present appears to form the design, in contrast to the darker red or blackish overlay. Several sherds retain the black color of the original design, whereas in the others this has faded to a brown or even a dull reddish color. One very coarse potsherd, apparently from a flat tripod vessel, has a dull white slip on the inside with broad, criss-cross red lines (pl. 9, *cc*). Aside from the Usulután type sherds this is the only painted fragment. This is similar to the red-on-white sherds from the old Playa de los Muertos horizon.

Among the heavier, coarser sherds occur examples of low, flaring, swollen lips; direct rims; broad, vertical loop handles, smooth rocker zigzags (pl. 9, *e*), and both fine and coarse incised decoration (pl. 9, *a, c*). At the present stage of preliminary analysis this coarser pottery shows no very striking differences from the monochrome or domestic wares associated with the upper polychrome horizons. The polished orange ware and especially the Usulután or related painted pieces are unique so far as this site is concerned. Aside from pottery the only other artifacts from these levels are a few fragmentary obsidian flakes (pl. 9, *k, m*) and a heavy, stemmed, pottery stamp with a geometric design (pl. 9, *l*). The stamp comes from P 8. The nature of the deposit below the sand level in the northern extension rather suggests the fringe of a midden whose concentration lay still farther to the north. Unfortunately, it was impossible to follow up this problem at the time, owing to the rapidly rising water level. These subsand layer ceramics at Santa Rita suggest definite affiliations with the oldest horizon at Playa de los Muertos.

PLAYA DE LOS MUERTOS (FARM II)

This important site is located on the east bank of the Ulna River close to the northwest corner of farm II (see map, fig. 5). In this general vicinity Gordon (1898) carried on extensive excavations in 1895 and 1897, and later, in 1929, Mrs. Dorothy Hughes Popenoe (1934; also see Vaillant, 1934) isolated the old Playa de los Muertos culture at this exact spot. For this reason we visited the site on January 18, 1936, the day after establishing our headquarters at Progreso. First impressions regarding the possibility of further work were extremely discouraging. The terrific flood of the preceding fall had removed most of the point where Mrs. Popenoe worked, as well as the entire island just below it (see map, Popenoe, 1934, p. 81). A small hard-pan or dense clay playa remained, on which we found a few Playa de los Muertos type potsherds. However, we found none

in situ on the adjacent steep banks, nor did we note any traces of burials or of polychrome pottery deposits in the vicinity. It was apparent that, at most, only a tiny remnant of the area worked by Mrs. Popenoe remained at the small playa previously mentioned. This opinion, based on comparison with Mrs. Popenoe's map, was verified by Mr. Roberts, overseer at farm 11, who had assisted Mrs. Popenoe in her work. For this reason we sought other sites, hoping to encounter elsewhere, the older type of Playa de los Muertos material in direct relationship to the polychrome horizons.

By the middle of April 1936 it was apparent that we were not going to find typical old Playa de los Muertos material at any of our other sites, despite the discovery of polychrome ware superimposed on pottery suggesting the Playa de los Muertos culture at Santa Rita (farm 17). For this reason, while work continued at Santa Rita, the senior author returned to the Playa de los Muertos site on April 17.

Subsequent to our first visit to the site, a large levee had been constructed along the river just east of the main site, and on the levee, and in the deep borrow pit or trench, we found numerous fragments of polychrome pottery. This material was concentrated at one place on the west wall of the borrow trench and here we later excavated (excavation 2). This site was only 80 meters southeast of the playa (with the old type sherds on its surface) which marked the eastern boundary of the grave area worked by Mrs. Popenoe. At this latter point close examination of the 4-meter bank behind the playa revealed a few sherds of coarse brown cooking ware and one tiny polychrome fragment *in situ*. Here excavation 1 was commenced.

Excavation 1, which was made on the very top of a point projecting out onto the clay playa, was L-shaped. The main cut was 2 meters wide and 6 meters from west to east. To facilitate handling the dirt from the deep cut, a north to south extension 4 meters long by 1½ meters wide and slightly more than 2 meters deep was made from the east end of the main cut south to a steep bank on that side. The north wall of excavation 1 is illustrated (fig. 16; also see Strong, 1937, fig. 79), and the position of the shallow north to south L extension is indicated by the shelf under skeleton 1. The main east to west trench attained a maximum depth of 6 meters. The soil layers from top to bottom are well indicated in the diagram (fig. 16). Potsherds were first encountered at a depth of 80 centimeters at the west end and 1.30 meters at the east end. Scattered sherds extended through this layer of gray clay (P 1, fig. 16) to a depth of 1.8 meters, where the sterile yellow clay began. The majority of these sherds

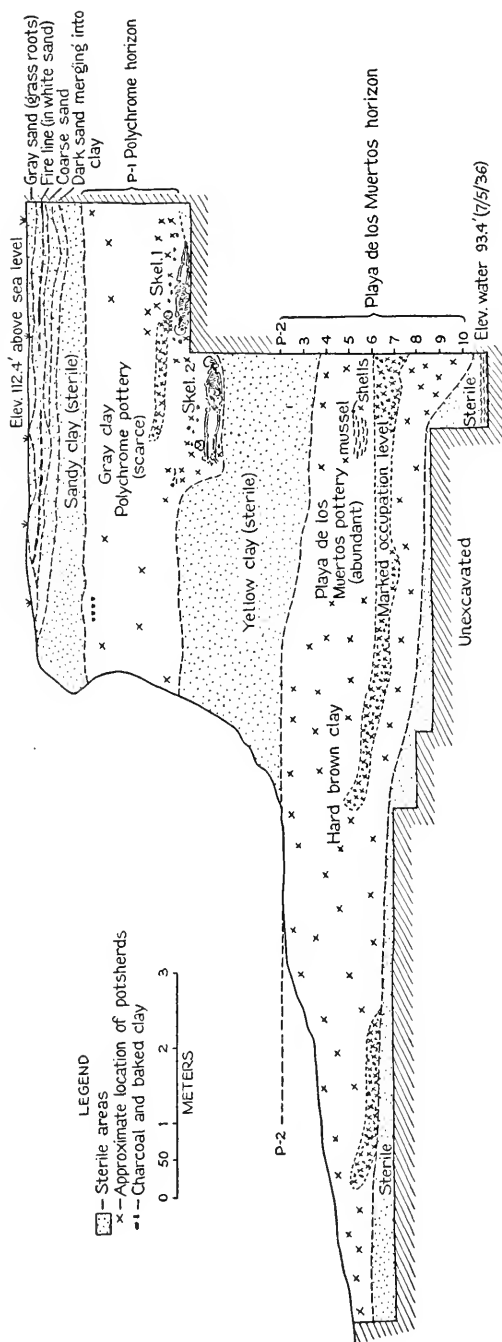


FIG. 16.—North wall of excavation I, showing stratification, Playa de los Muertos (farm II).

were from monochrome red to gray cooking ware, but enough polychrome sherds were found to establish the horizon as definitely belonging to the polychrome period. Sherds were too scarce, however, to make 30-centimeter levels of value, so that the entire stratum was designated P 1. Two extended skeletons occurred at the bottom of this horizon (fig. 16). Each was accompanied by a broken monochrome cooking pot, but definite polychrome sherds were also found next to each skeleton. Skeleton 1 had, in addition, an obsidian flake knife and a perforated pottery labret or ear plug. Below these skeletons we ran into a layer of yellow clay which was absolutely sterile. At a depth of 3.35 meters more sherds of a different type (Playa de los Muertos culture) were encountered coincident with our passing from the yellow clay into a hard brown clay. Owing to their abundance, it was now possible to work by 30-centimeter levels, thus P 2 (pottery level 2) began at this point. The Playa de los Muertos horizon (P 2-10, fig. 16) sloped down from west to east. As indicated in the cross-section (fig. 16) at least one and possibly two definite occupation or house floor levels, marked by black soil, concentrated charcoal, animal bones, sherds, etc., and a small deposit of mussel shells, were encountered. Owing to the depth of the deposit and to lack of time, it was impossible to work out these living levels beyond the walls of the excavation. No post holes were encountered, but baked clay with wattle and daub impressions was fairly abundant. In the west end sterile soil underlay P 6, but in the east end the occupation strata dipped to the top of P 10, terminating just above the then level of the river (fig. 16).

It is obvious, both from the direct superimposition of the two ceramic horizons separated by a barren stratum (fig. 16) and from the markedly different ceramic content of each, that two distinct cultures are represented at this site. Of these, the lower or Playa de los Muertos horizon is the older. Since this horizon extended well to the west prior to the recent flood and since the main concentration of the upper or polychrome horizon occurred on a similar level 80 meters to the southeast (excavation 2), it would appear probable that only the edges of the two occupation levels overlap at excavation 1 (fig. 16). For the purpose of obtaining direct stratification, we were therefore extremely fortunate in choosing the place for our main trench.

Excavation 2, in the west wall of the levee borrow-pit, was small but yielded a considerable amount of polychrome pottery. The excavation was 5 meters from north to south and slightly less from east to west. The first potsherd was encountered at a depth of 70 centimeters and the lowest at 2.40 meters. No noticeable changes

in polychrome pottery types were observable in this deposit, and 30-centimeter levels were not recorded. Abundant polychrome sherds were scattered throughout a gray to brown clay stratum. The pottery level contained concentrations of ash, charcoal, and sherds, one lenticular hearth, numerous small boulders, and abundant sherds. Below the pottery level an absolutely sterile, brown sandy clay was encountered. The maximum depth of this excavation was 3 meters. In absolute level the polychrome horizon at excavation 2 compared closely with the upper or polychrome horizon (P 1, fig. 16) at excavation 1.

Excavation 3 was made on the northern side of the playa in the same dense brown clay level where old Playa de los Muertos material occurred in the main trench. At excavation 3, this level was on the surface, owing to the removal of the top soil by the river. An excavation 6 meters long (from northeast to southwest) and 1.5 meters wide was carried down to a depth of about 1 meter. No sherds or other artifacts were encountered below the surface and, as it was apparent that we were outside the area of ancient occupation, work was stopped.

Before describing the artifact content of the various levels at excavation 1, it will be well to discuss briefly the material from excavation 2. All the ceramics (other artifacts were extremely rare) from excavation 2 correspond with those from the A (P 1), the upper or polychrome level at excavation 1. These two horizons are actually on the same level, and since material was scarce in A (excavation 1) and abundant in excavation 2, the latter must be considered in order to define the polychrome wares characteristic of the upper horizon. Owing to the apparent uniformity of all wares exposed in the cut bank at excavation 2, it was considered as one unit. To check this, however, material from the very bottom portions was segregated for comparison with the remainder. This will be discussed after the bulk of the material has been analyzed.

The domestic ware from excavation 2 is predominantly monochrome, of a dull red color. A much smaller number of sherds have traces of crude linear designs in brown, dark red, or black. The bulk of the domestic sherds appear to be from medium large vessels which were fairly well polished, with openings varying from heavy direct lips to slightly flaring rims. Vertical, solid, loop, and strap handles occur frequently. There are two dimpled bases and one partially hollowed, conical foot (from a unique vessel form). Six monochrome sherds are decorated with well-executed but simple incised geometric designs.

Nine rim sherds from finer vessels that were both painted and incised are of the thick Las Flores vertical-walled vase type (compare pl. 5, *a-c*). These have a polished slip ranging from dark red to orange, a band of black geometric designs under the lips and below this another band of incised design. As indicated earlier, this Las Flores type of incised and painted ware is also represented on the Bay Islands (Strong, 1935, pl. 18, *b, c, e*). The sherds of this type from excavation 2 (farm 11) also have inner and outer design elements that rather definitely suggest Bay Island Polychrome I pottery. One other sherd with more delicate painted and incised designs (similar to pl. 5, *h*) indicates the same fusion between the Las Flores painted and incised vase style and the Mayoid painted style that occurred at Las Flores. At excavation 2 (farm 11), as at Las Flores, the Mayoid polychrome type of vertical vase is the more numerous. Sherds from these vases are very similar to those from Las Flores (compare pl. 5, *f-m*). They are relatively thick (compared to the vases from the lower levels at Santa Rita) with elaborate but conventionalized over-all designs in red and black on yellow buff. Geometric motifs such as crossed circles are also common. One flat bottom, one low, round, solid, tripod leg, and one thin, solid, rectangular, tripod leg occur. Two elaborately sculptured sherds have a curvilinear Mayoid design. One vestigial spout (identical with pl. 6, *b* from Las Flores) is from a painted and incised vessel.

Smaller bowls with black and red designs on light red or orange are even more common than the Mayoid vase type. Some of these have conventionalized "Mayoid" figures but more have geometric designs such as lines and circles. They are small to medium in size including direct bowls, small pots, and small vases. One vertical strap handle, one flat bottom and numerous rounded bottoms occur. In style these vessels represent a blending between the Mayoid and the Bold Geometric with the latter style predominant. Tripod plates and dishes are lacking here as was true at Las Flores (excavation 2).

Bold Geometric ware is fairly common and the large swollen vessel with broad strap handles occurs (like pl. 7, *a*). The monkey lug, however, is absent at this site. The slip of these pieces is a very dark polished red or orange with geometric designs in black. Animal design forms are lacking. One sherd of this type has a geometric design in white paint. Two typical deep dimple bottoms occur. No figurines, stamps, or whistles were found, but there is a brown pottery foot from a rather large hollow effigy. Two fragmentary prismatic flakes of obsidian were the only other artifacts.

The material segregated from the lowest level in excavation 2 contains fragments of all these types and establishes the uniformity of the deposit. The domestic ware is identical, numerous pieces having blotchy dull red or brown designs. One well-polished sherd has a flange outside the neck with a dull red criss-cross design extending from flange to body. One sherd represents the Las Flores type painted and incised vertical vase. There are several small bowl fragments with conventionalized Mayoid and geometric designs, and one typical Bold Geometric swollen bowl fragment. A sample gathered from the surface of the borrow-pit is similar but contains several "Mayoid" vertical vase fragments rather suggesting the Bay Island Polychrome I type (Strong, 1935, pl. 21 and fig. 21). A portion of a very small tripod vase with red slip and black line decoration has an outer wall panel with excellently sculptured Mayoid faces in profile. In general, all the material from excavation 2, Playa de los Muertos, agrees very closely with that from excavation 2, Las Flores, and with pottery levels A and B in excavation 1, Santa Rita.

Returning to excavation 1 at Playa de los Muertos, we will first consider the material from P 1, the upper or polychrome horizon (fig. 16). The fairly abundant domestic ware is identical with that just described at excavation 2. Two restorable vessels of this type accompanied the two burials in the lower portion of P 1 (fig. 16). That with skeleton 1 is a round-bottomed pot with a low flaring rim and two vertical round handles. It is of coarse brown, unslipped ware with triangular incised designs over the lower neck and upper body. The vessel with skeleton 2 is a polished black vessel with a direct rim and three small solid legs. In direct association with the coarser ware throughout P 1, polychrome sherds occurred. The majority of these are small and some of them are eroded, but their type is definite. The majority come from small bowls with a red or orange slip. The lips of these sherds are painted red or black and similar linear designs occur on the body of the vessels. Ten small sherds are colored buff to orange and have remnants of complex red and black designs. Two orange sherds with red lines and large dots suggest the Bold Geometric ware. Two polychrome sherds are from flat bottoms, and one is a rounded flat bottom. One large, hollow, cylindrical leg with an orange slip and red and black designs is from a tripod dish. The leg has a vertical perforation in the lower portion and holes in the part joining the body. It originally contained a rattle. This type of vessel (compare pl. 7, *e, f*) was lacking in excavation 2. The only other artifact encountered was a fragmentary prismatic flake of obsidian. Although

the polychrome sherd sample from excavation 1 is small, it is very similar to the material from excavation 2.

Playa de los Muertos culture material is abundant throughout an average of 2 meters in the lower portion of excavation 1 (P 2-9 inclusive, fig. 16). Broken pottery comprises the bulk of the collection, since no complete vessels were recovered by us and other artifact types were rare. This discovery of undisturbed refuse deposits entirely pertaining to the old Playa de los Muertos culture is exceptionally important. Not only does it give a representative and unselected sample of the culture but it also permits the inclusion of burial materials obtained by Gordon and Popenoe as definitely pertaining to the older horizon. Although Gordon in his brief published report gives no data on relative depths and states that no observable stratification occurred (1898, p. 38), it is undoubtedly significant, that the majority of complete vessels he illustrates (1898, pl. 7, *a, b, c, d, e, h, k, n, o, p, q, r, s, u*) are characteristic of the older Playa de los Muertos culture. Furthermore, examination of his letters from the field and the occasional depths he recorded in cataloging, now on file in the Peabody Museum, indicates that all these complete vessels came from the lowest portions of his Playa de los Muertos (Largartijo) excavations. These undoubtedly were from burials of the old Playa de los Muertos period. The old burials excavated by Mrs. Popenoe are fully documented (Popenoe, 1934, pp. 65-79). All are from below 4 meters in depth and contain only Playa de los Muertos materials. Since we found no entire vessels of the Playa de los Muertos culture, we have included outline sketches of vessels obtained from graves by Mrs. Popenoe (figs. 17, 18). Thus, each ware or ceramic subtype of this culture, established on the basis of our potsherd collection, can be illustrated in its complete form by a vessel from Mrs. Popenoe's collection pertaining to the same Playa de los Muertos type or subtype (also compare Mrs. Popenoe's illustrations, 1934, figs. 2, 6, 8, 11, 12, and 15). The final description of the Playa de los Muertos cultural horizon must include a complete study of the abundant comparable Gordon and Popenoe materials, but this is not attempted here.

For present purposes we have grouped our 30-centimeter stratigraphic levels of Playa de los Muertos culture material (fig. 16, P 2-9 inclusive) into two uneven divisions, an upper (P 2-4 inclusive), and a lower (P 5-9 inclusive). The lower grouping of levels, which we may call levels C (P 5-9), yielded almost twice as much material as did the upper levels, here designated as B (P 2-4), owing to the fact that level P 5 was unusually rich and overweighted whichever half it was placed with. This discrepancy can be avoided later when

finer analyses are attempted, but for present purposes this segregation into a smaller upper and later grouping of Playa de los Muertos cultural materials (B); and a larger, lower, and earlier grouping (C)

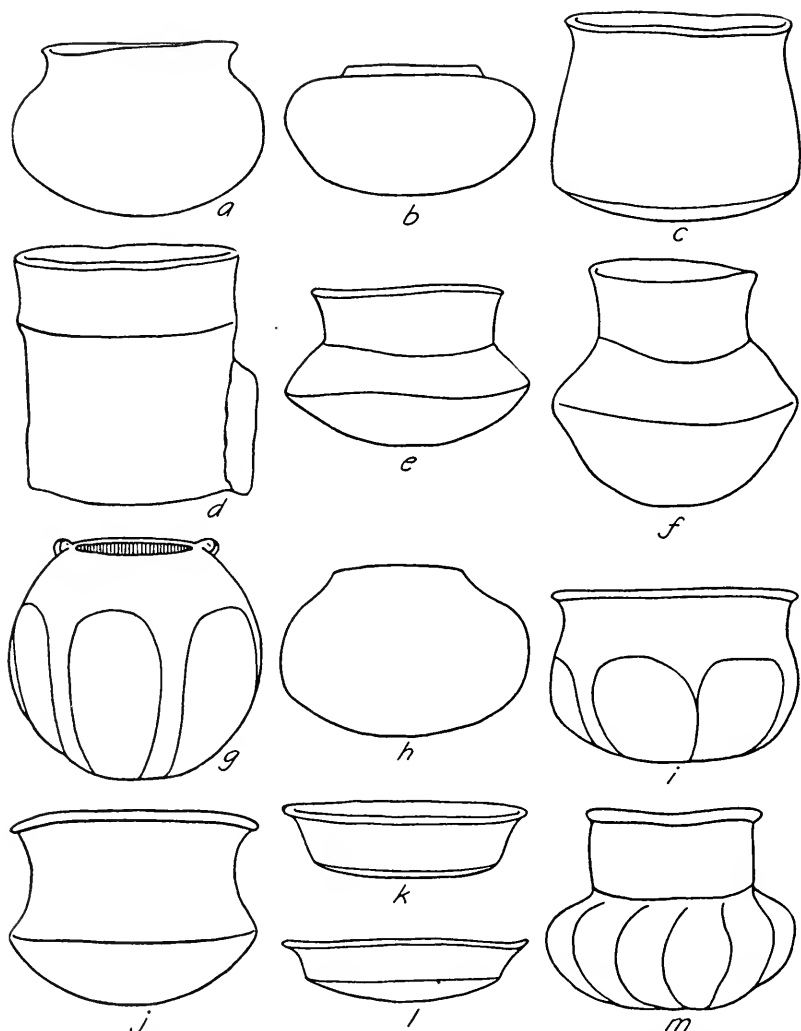


FIG. 17.—Outlines of vessels of the Playa de los Muertos culture obtained by Dorothy H. Popenoe. Not to scale. *a*, burial 2; *b*, *c*, burial 4; *d-l*, burial 5; *m*, burial 7.

must suffice. Even such an arbitrary division suggests certain ceramic trends within the period that may well be significant.

The ceramic materials from B and C fall into six main wares or ceramic subtypes based on surface finish or decorations (pls. 10, 11,



FIG. 18.—Outlines of vessels of the Playa de los Muertos culture obtained by Dorothy H. Popenoe. Not to scale. *a*, burial 7; *b*, *c*, *d*, *e*, *f*, *i*, burial 8; *g*, *h*, *j*, *k*, *l*, *m*, burial 11.

and figs. 17, 18). Each of these subtypes share common features of form and decoration uniting them into a very definite major ceramic type characteristic of the Playa de los Muertos culture. The most abundant sherds from both B and C may be described as (1) *unslipped, rough, brick-red to sooty gray ware*. These are often from large vessels with slightly flaring rims and necks of variable height, or from smaller vessels with low necks and swollen lips. Broad, vertical, strap handles are common in both B and C, but the great majority of handles in C have two or three vertical ridges and corresponding depressions down the outside. Two round, solid, vertical handles of large size from B and one from C have conical tenons on the ends for attachment to the body of the vessel. Of the nine basal fragments of this ware in B, eight are flat and one dimpled; in C three of the four basal sherds are flat and are slightly rounded. One spout of this ware occurs. Decoration is rare, several sherds have incised lines forming criss-cross designs, and three sherds have a raised ridge with regular indentations about the greatest diameter of the vessel. Subtype 1 seems very similar to the plain or domestic wares characteristic of the upper or polychrome horizons at Playa de los Muertos, but the prevalence of flat bottoms seems rather distinctive. Owing to lack of space, this subtype is not illustrated here except for an outline sketch (fig. 17, b).

Subtype 2, (pl. 10, a-h), *slipped and polished orange-red to brown ware*, is almost as abundant as subtype 1 in B, but only about one-fourth as abundant in C. Shapes in subtype 2 are very similar to those in subtype 1, but the vessels were somewhat smaller (fig. 17, g, h, i, j, and fig. 18, e, g, i, j, k). One spout from this sub-type is from B and 2 from C. A rather heavy basinlike bowl or vase (fig. 17, k, l, and fig. 18, c) is rather common, as are direct bowls (fig. 18, g, l). Handles seem rare but a few vertical strap handles occur. Fluted sherds (pl. 10, f) are fairly abundant in B but do not occur in our sample of this ware from C. Fluted fragments are usually from the body portion of rather small rounded or swollen bowls (like fig. 18, m, in shape). The fluting varies in width and is either vertical or diagonal. Incised lines often set off the fluted portions. Incised and modeled sherds of this type occur in B, but only incising in C. Several fragments from B have intricate and well-executed geometric and curvilinear incised designs (pls. 10, 11). In C basinlike bowls with heavy incised designs are represented. In B a hand in high relief is the best modeled piece. Broad, flattened lips with deeply incised decoration (pl. 10, h, i represents the type) are very common in B and fairly common in C. Usually the entire rim is flattened and decorated, the rim ex-

tending farther out on two sides, forming a handle or a definite tab (pl. 10, *h, i*).

Subtype 3 is a *dark gray to black, highly polished ware* (pl. 10, *i-n*; figs. 17, *m*; 18, *m*). This is a very distinctive slipped ware with such a high polish and so much fire clouding that certain pieces have an almost purplish color. The forms are very similar to those in subtypes 2 and 4, and fluted sherds and flat, heavily incised rims (pl. 10, *f, h, i*) are common to all. Fragments from basinlike bowls are common (pl. 10, *j, m*) and the incisions on such pieces are sometimes so deep as to suggest a series of outer flanges. There are no handles of this ware, but one small, solid, cylindrical foot occurred in B. This is the only foot noted in the entire Playa de los Muertos culture horizon. Material of subtypes 2 and 3 are about equal in amount but subtype 3 is more abundant in C than in B. This suggests that subtype 3 is generally earlier than subtype 2.

Subtype 4 is a *slate-gray to buff, highly polished ware* (pl. 10, *o-s*; fig. 17, *d, e, f, k*; fig. 18, *a, b, f*). In amount this ware is about equal to the two preceding subtypes and is slightly more abundant in C than in B. The majority of pieces appear to have had a light-colored slip and a subsequent high polishing that gives them almost a glazed appearance. The paste is exceptionally fine, and the pottery very hard. Irregular dark firing clouds are very common (pl. 10, *r*). In general the shapes are similar to those already discussed, but small bowls with low, slightly flaring and swollen lips are common (pl. 10, *o, q, s*). Several sherds have ridges, tabs, and human features in relief, and a number of spouts of this ware occur in C. An unusual flaring, trumpet-like neck has been figured elsewhere (Strong, 1937, fig. 76, upper left). A fragment similar to this was found in the older deposits at Lake Yojoa by Mr. Rittenhouse and erroneously restored as a trumpet. Flat bottoms are common, but a few rounded bottoms occur. Handles are rare.

Subtype 5 may be designated as a *ware with a chalky white wash* (pl. 11, *a-c*). It is relatively rare in both levels but somewhat more abundant in C than in B. It should be noted that the majority of the figurines from B are of this ware (pl. 11, *q, r*). The majority of sherds come from heavy, direct bowls or from pots with low necks and slightly flaring lips. One extremely broad, vertical strap handle occurs, as well as two large spouts (pl. 11, *a*). The figurines and a few sherds of this type with painted designs will be discussed later.

The sixth ceramic subtype from this horizon is comprised of various *painted wares*. Painted pottery is relatively very rare in the Playa de los Muertos culture horizon, yet forms an important and varied

type. It was about equally divided between B and C, perhaps indicating that it was more abundant in later times since the smaller upper section yielded an equal amount of painted sherds. Red and black painted sherds constitute one type (pl. 11, *f, g, k*). Some of those sherds have alternate areas of black and red sometimes separated by incised lines (pl. 11, *g*). In other cases these red and black areas are very irregular, and the colors form irregular blotches rather than controlled designs. Numerous flattened and incised rims of the very dark subtype 3 have flecks or small areas of red paint (pl. 11, *f*), others have red on black, or black on red, painted areas. The under side of such flattened rims are usually black. Several fluted fragments have black and red painted areas. A few small vertical handles and one very small horizontal handle (pl. 11, *g, k*) occur in this red and black ware. The red and black painted sherds are more numerous in B than in C. Red on buff sherds are the next most abundant type (pl. 11, *i, j, o*). The majority of red on buff sherds come from C, but the type is represented in B. Most of these sherds come from small vessels with a red band on the inside and outside of the rim (pl. 11, *j*). The lower portions and the bottoms of these vessels were often red, and the remainder, except for red rims, was buff. Several have incisions in the red area showing the underlying buff. One rim sherd from a direct bowl, polished red on the outside, has faint red linear designs on the inside with the lighter buff showing through them like negative painting. A very well-modeled and painted red and buff lug comes from B (pl. 11, *o*). Several large sherds of coarse unslipped brown or buff ware have red bands on lip, neck, or rim (pl. 11, *h*). Two sherds in B and four sherds in C have a dull white slip with red lines or bands on the outside and in one case on the inside (pl. 11, *m, l*). They are from large vessels with low flaring lips and include one broad, vertical strap handle. Three sherds from B and one sherd from C have irregular white designs on a red painted background. These are from large, coarse vessels. In two cases the lip has a band of white inside and out; in one there are broad, irregular vertical lines extending down the rim, and in another there are blotchy white designs on the inner surface.

One polished, dull red rim sherd (pl. 11, *n*) has vertical lines of dull gray paint extending down the neck. This suggests negative painting, owing to the fading of the gray paint. It has already been stated that several of the other painted sherds with faded linear designs imitate negative painting. In passing it may be said that although Usulután ware is not present in our Playa de los Muertos culture ceramic sample, it does occur at the site (Vaillant, 1934, p. 90).

Gordon obtained an excellent complete vessel of this ware at a depth of "26 feet" (Peabody Museum C 1054), and we found sherds of Usulután ware in the lowest horizon at Santa Rita (farm 17). It is probably one of the components of this early ceramic complex. In concluding this brief description, it is interesting to note that whereas the polished and incised ware of the Playa de los Muertos culture is of an advanced and mature type, the very small percentage of painted wares is highly variable and suggests an early, experimental interest in this technique.

Of the remaining artifact types, the figurine fragments are perhaps the most interesting. From B come four fragments, all from hollow figurines and all but one with a polished white slip (pl. 11, *v, r*). Three of these, all with a polished white slip, represent a bulbous, seated type that is much conventionalized (pl. 11, *v, r*). The fourth is an unusually well-modeled face of polished brown ware (pl. 11, *p*). From C come 10 figurine fragments, all of which are solid and all but one without any slip. Three represent female torsos (pl. 11, *t, u, v*). Although very simple, they have a primitive naturalism that is rather pleasing. Six fragments of solid figurines are more fragmentary but suggest similar types. Gordon (1898, pl. 10, *d, f, g*) shows complete examples of this solid, naturalistic type. The last fragment is also solid but has a dull, polished white slip like those from the upper level (pl. 11, *s*). Our sample is too small for certainty, but there is at least a hint that the hollow, slipped figurines were later, being preceded by the solid, naturalistic, hand-modeled type.

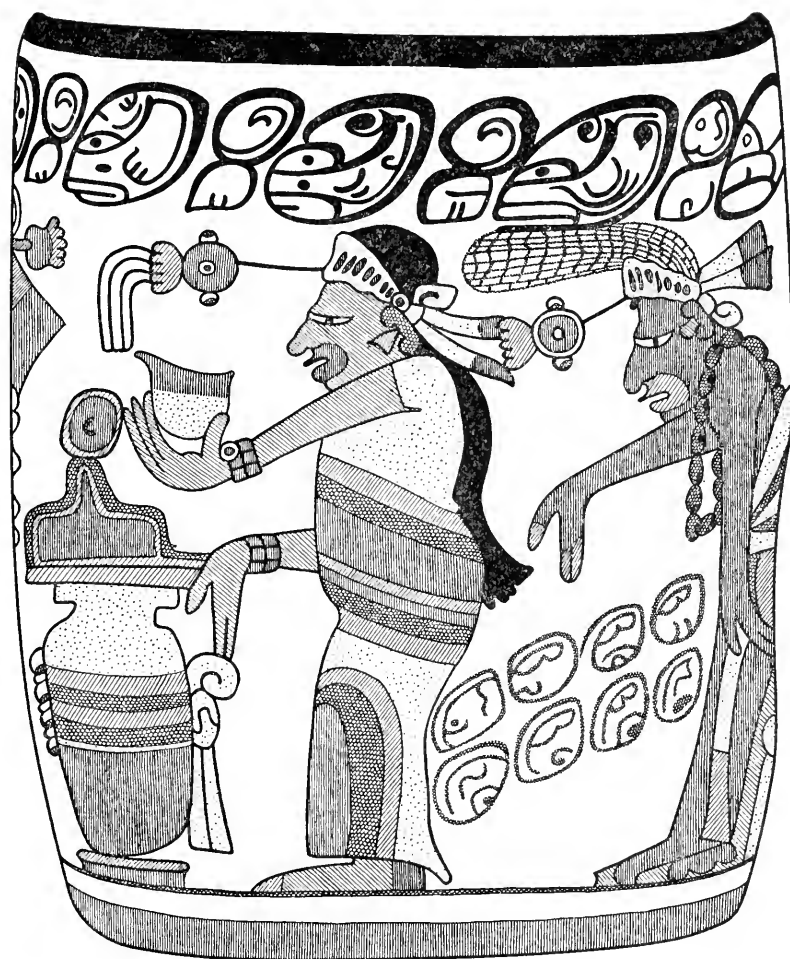
Artifacts of materials other than clay were very rare. B yielded one small jade bead, four fragmentary prismatic flakes of obsidian, two retouched pieces of obsidian, two polishing stones (one stained red), one piece of pink chalk (?), and two irregular flakes of hard stone. C yielded one prismatic flake of obsidian, one small rectangular muller, and several battered hammer-stones. As is true of the later horizons, the proportion of perishable to nonperishable artifacts, other than pottery was very low in the Playa de los Muertos culture. It is interesting to note that animal bones were unusually abundant in this horizon, suggesting a considerable dependence on hunting. Over a dozen fragments of baked clay retain the impress of wattle and daub house construction. When the present midden material is considered in relation to the much more elaborate grave materials obtained by Mrs. Popenoe (1934) and by Gordon (1898), a reasonably complete record of the period is available.

OTHER SITES

In addition to the sites intensively worked, numerous other mounds or refuse deposits were also examined. The majority of these are shown on the map (fig. 5). Mound groups are abundant on both sides of the Ulua River but to date have yielded relatively little material. Aside from superficial examination and the gathering of small sample sherd collections, we did no work at such sites. In general, the mounds on the present valley floor appear to be relatively recent and yield ceramics that are inferior to those of the earlier polychrome periods. However, until adequate work has been accomplished at such sites, the linkage between definitely historical sites, such as Naco, and the deeply buried, earlier polychrome periods will be obscure. Our failure to excavate mounds was due to lack of time, not of interest. Small excavations were made at two polychrome sites, one below Naranjo Chino and the other on farm 15 (see map, fig. 5). These yielded splendid polychrome sherds apparently contemporaneous with the lower levels at Santa Rita (farm 17). On farm 10 we excavated a shallow polychrome deposit containing pottery identical with that from the late polychrome horizon at the nearby Playa de los Muertos site (see map, fig. 5). It is probable that earlier polychrome deposits occur here also as indicated by the excellent, realistic Mayoid vase (fig. 19) which is reported as having come from farm 10. We have illustrated this specimen, which is in a private collection near Trujillo, because it is a splendid example of the best Mayoid tradition in early Ulua-Yojoa polychrome wares (compare pls. 1 and 8, *a*, *b*, also fig. 30). It is also unique in showing ceremonial drinking among the Maya.

NORTH END OF LAKE YOJOA

On February 22 and 23, 1936, Mrs. Strong, Dr. Wilson Popenoe, and the senior author stopped over at Jaral and visited sites east and west of that town where commercial excavations had been carried on (see map, fig. 20). At Aguacate we obtained a considerable amount of broken but restorable pottery that had been discarded by these earlier diggers. On March 9, Mr. Paul, Mrs. Strong, and the senior author returned to Jaral and remained there until April 6, carrying on excavations at various polychrome sites in the hope of obtaining at least a partial scientific record prior to their entire destruction by pot hunters. Our work was interrupted by "Holy Week" during which period neither work nor travel was practicable. Later, on May 26, Mr. Paul returned for a week in order to carry on deeper excavations,



0 ————— 5
cm.



FIG. 19.—Polychrome vase of Ulua Lower Mayoid type, said to have been found downstream from Playa de los Muertos on the Ulua River bank. (From a private collection near Trujillo.)

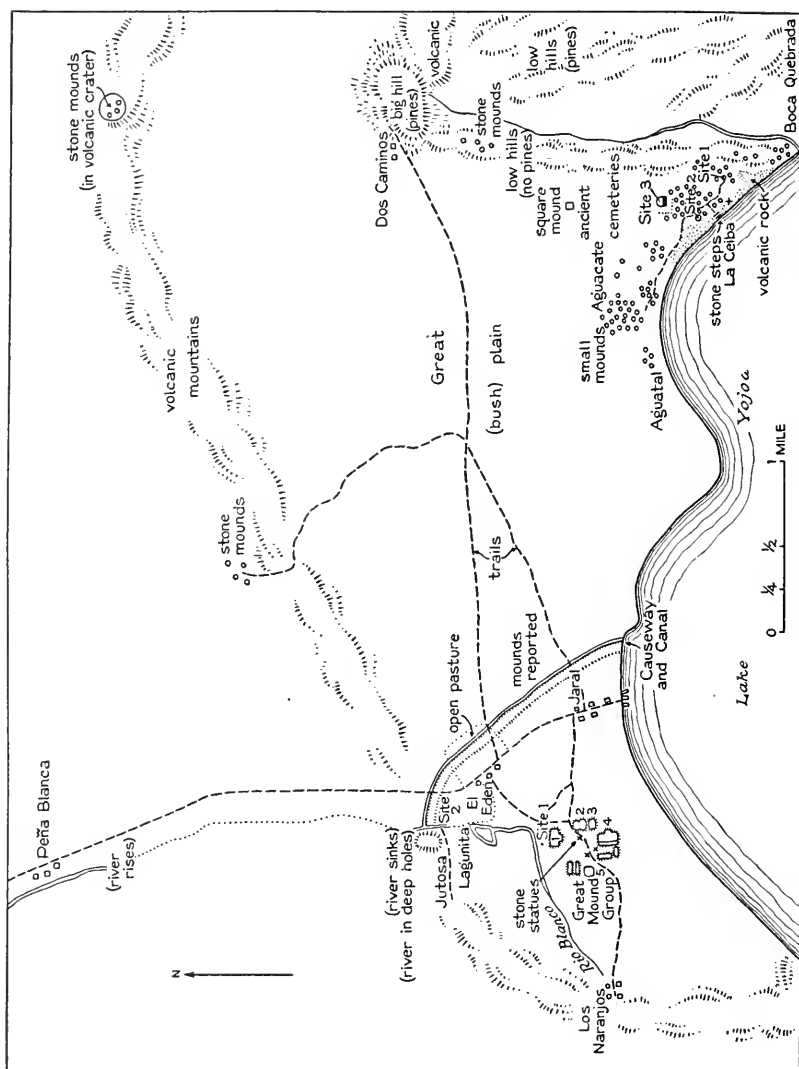


FIG. 20.—Sketch map of archeological sites around the north end of Lake Yojoa.

seeking an earlier type of culture at the Los Naranjos site. In this venture he was successful despite the very limited time available.

Only within the last 4 or 5 years has the occurrence of prolific mounds around the north end of Lake Yojoa become a matter of scientific knowledge. The first of these were dug up by local farmers and, later with the permission of the Honduras government, J. B. Edwards carried on extensive excavations in the region. In 1934 Mrs. Doris Zemurray Stone¹⁴ visited Los Naranjos and published a brief report.

In 1935 Frans Blom, Dr. Jens Yde, and Prentiss Andrews spent 4 days around Jaral in the course of the Tulane University-Danish National Museum Expedition.¹⁵ They explored around the various sites, worked with Mr. Edwards, and from him obtained collections of the polychrome ware.

On our second visit we rented a dilapidated house in Jaral and boarded at the "Grand Hotel Rats' Nest", as it was fittingly christened by Yde and his companions. Our genial host, "El Chino Alejandro", however, made us as comfortable as his limited resources permitted. In Jaral we were also greatly aided by Capt. Evalyn Bush, and in the field by our two main workers, Paco Ramirez, of Dos Caminos, and Miguel Hernandez, of El Eden. Information furnished by Mr. J. B. Edwards proved very useful throughout our work.

The major geographic characteristics of Lake Yojoa have already been touched upon. Outstanding archeological features of the plain at the northern end are, first of all, the great mound group and fragmentary stone statues at Los Naranjos (great mound group, map, fig. 20); next the long earth mound or causeway, with its parallel ditch, just east of the road to Jaral (map, fig. 20); and finally the series of "ancient cemeteries", or low house mounds containing burials, about 3 miles east of Jaral near the lake shore (map, fig. 20). In the following account we will attempt to present very briefly the major characteristics of certain of these features, each of which merits at least a full season's work and a complete report. Our primary aim was to determine the nature and association of the major ceramic wares present at such sites and, if possible, to determine whether stratification of culture horizons might be present. The apparent richness

¹⁴ 1934, pp. 123-128. Mrs. Stone, p. 128, mentions the occurrence of gold at this site. To the best of our knowledge, no metals of any kind have ever been found there.

¹⁵ See Yde, 1935, and 1936. The earlier report (fig. 5) shows four typical Yojoa vessels; the upper has the "dancing figures" and is Mayoid in type. The three lower vessels are in the local Bold Animalistic style.

and complexity of Lake Yojoa ceramics makes any brief description extremely difficult. However, since the majority of Yojoa collections in various museums are highly selective, even a preliminary account of the manner in which the various types of vessels and artifacts occur *in situ*, should have value. Since complete or restorable pottery vessels are more abundant in Lake Yojoa sites than in those previously described, we will discuss them in this preliminary report, leaving detailed potsherd analysis for a later time.

AGUACATE AND AGUATAL

Modern place names around the north end of the lake are usually derived from certain trees that mark favorable areas for milpa farming. Aguacate and Aguatal (map, fig. 20) are so named, and it was here that the first finds of Yojoa polychrome pottery were made. Both sites have been sadly looted, and though we visited them on our first trip to the lake, we were unable to find any mounds or promising areas sufficiently undisturbed to merit scientific excavation. Probably a very large proportion of Yojoa polychrome vessels in collections inside and outside Honduras, have come from these sites which appear to have been exceptionally prolific. We reached them after a long walk along the trail to Dos Caminos (map, fig. 20), then cutting south through the generally low but very dense bush. Each site consists of a large (Aguacate is the larger) irregular area covered with low mounds ranging from barely visible eminences to some 2 meters high. Originally, the mounds were covered with rocks, many of large size, but at the time of our visit both areas were entirely covered with shallow, irregular burrowings and piles of rich black dirt and stones which obscured almost all natural contours. The dense bush added to the difficulty. The excavations ranged from 30 centimeters to about 2.5 meters in depth and, starting in what originally seem to have been mounds, run labyrinthian courses wherever the machete-wielding "huaqueros" believed they were in mixed soil. Potsherds were abundant, polychrome pieces seeming to predominate over plain or cooking ware fragments, and a number of splendid and only slightly broken vessels lay about, indicating that they had been carelessly excavated and then abandoned in favor of harder and more resistant complete vessels. Numerous three-legged metate fragments of various sizes, roller pestles, rectangular mullers, and two large polished celts were noted. There were no human bones in sight, but our guide said that small fragments were occasionally encountered in association with complete vessels. Among the great number of rough, volcanic rocks

that once formed these mounds we noted a few that appeared to be artificially squared or smoothed, and in one or two cases the disturbed rocks appeared to have once formed part of some simple artificial structure.

Although the occurrence of some domestic pottery and broken artifacts, such as metates, suggests human habitation at these sites, the predominance of elaborately painted sherds and the reported occurrence of very numerous deposits of complete polychrome vessels suggests a burial ground wherein the human bones had vanished owing to the damp, very humous soil. In the light of our later excavations at La Ceiba and Los Naranjos, it seems probable that both habitations and burials formerly occurred here, with the latter coming to be predominant before the sites were finally abandoned. Except that Aguacate covers a larger area than Aguatal, and that the rather closely adjacent sites have been given different names by modern farmers, the two seem to be identical in types of pottery represented, in the nature of the mounds, and in the complete manner in which they have both been looted.

An analysis of all the vessels from, or reported to be from, these two sites would probably run the complex gamut of Lake Yojoa polychrome ware. Sherds of almost every Yojoa polychrome type were actually present in the old excavation pits, confirming the reports of various of the diggers that the majority of these vessel types occur in association. Our necessarily brief discussion of ceramics from these two sites is based, first, on 14 broken but restorable vessels which we ourselves picked up in the diggings at Aguacate on our first visit. Although these abandoned pieces may not represent the finest types from the site, they are definite as to site provenience and probably generally representative. Next, we were able to acquire a number of complete vessels obtained by local diggers at Aguacate and Aguatal, and in some cases to sketch and photograph other vessels from these sites which were not acquired (for example, fig. 30). Complete vessels thus obtained were sent to the National Museum of Honduras at Tegucigalpa, and our present illustrations were made from field photographs and sketches. Some of these latter vessels, reported to be from Aguacate and Aguatal, but not excavated in our presence, may have come from La Ceiba. However, we talked directly to the excavator of each, and there is strong probability that the majority did come either from the place designated or from one of the adjacent south-eastern sites (see "ancient cemeteries", map, fig. 20).

The 14 restored vessels we obtained at Aguacate fall into five major types in regard to form: first, straight-walled or only slightly flaring

vases or jars, with or without tripod feet; second, tripod dishes; third, open bowls with dimpled bases; fourth, two-handled pots with dimpled bases; and, fifth, bichrome or monochrome pots with direct or slightly flaring rims and two or four vertical handles. The finest of the first type is a vertical-walled vase with three slightly hollow, low, cylindrical feet. In form and coloring it is almost identical with one illustrated (pl. 1). It has the identical step and scroll design pattern on the lip, but the body design consists of two pairs of interlocked horned or

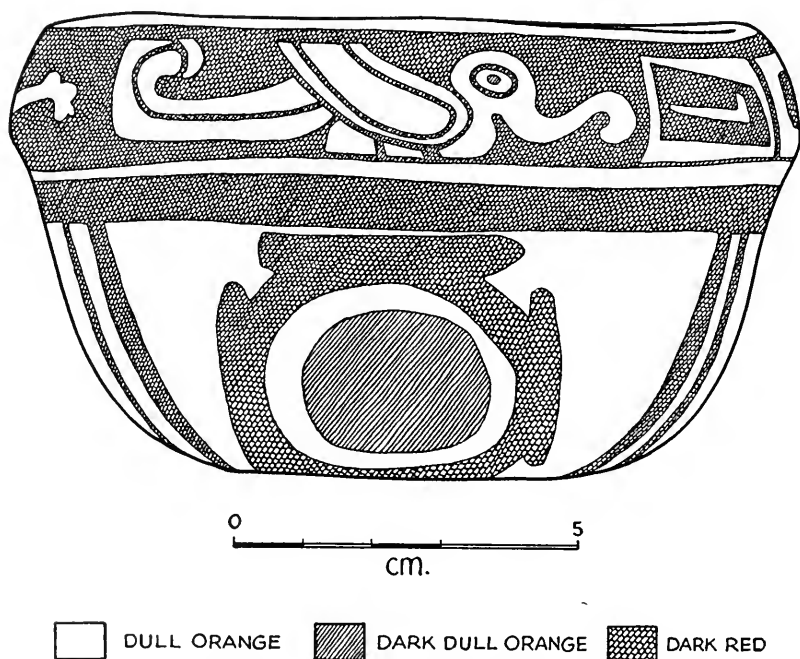


FIG. 21.—Yojoa Polychrome bowl, Bold Animalistic type, Aguacate. (Specimen in the National Museum of Honduras at Tegucigalpa.)

plumed serpents with spearlike flames coming from their nostrils (similar to pl. 13, *d*). A low, flat-bottomed vase with thickened lips and paneled walls is too badly eroded to make out the design. A third piece of this general type has slightly flaring, straight walls and a dimpled base. Around the neck is a band of skeuomorphic glyphs, dark red and black on an orange background. On the orange body of the vessel there are two conventionalized parrots in dark red and black. Tripod dishes, the second type, are here represented by only one example (pl. 14, *c*). This is of medium size with hollow, cylindri-

cal legs containing rattles. The body color is dark orange with panels of geometric and conventional designs in red and black.

The third type, bowls with dimpled bases, includes five vessels; the finest of these is of thin ware with a light orange background and elaborate design in dark red and black on the outside. Around the neck is a series of plumed Mayoid faces conventionally but exquisitely executed; these are identical with those on a very similar vessel from Aguatal (pl. 12, *c*). The body has complex, human figures in the same elaborate style, but erosion prevents a clear understanding of the design. A smaller thicker bowl with a buff background has purple around the lips and on the body, enclosing buff circles in which are crude, conventionalized Mayoid faces. Around the neck is a buff band with black, skeuomorphic glyphs. A heavy bowl has a white slip with massive, dark red, dull orange and black panels, bands, and designs. On the sides are two heavy monkeys squatting in profile. One has a forward-sweeping plume similar to those on the priestly figures, the other has a backward-sweeping plume and a long tongue. A thick but well-executed bowl is light orange with dark orange and black designs. On the rim, these are geometric, but in two circular areas on the side are ornate birds, evidently the Muscovy duck, with strange, wrapped objects on their backs. The last open bowl is light orange with two extremely ornate black and purple birds. It has isolated black stepped scrolls outside the lip (like pl. 1).

There are two vessels of the fourth type, i. e., bowls with two vertical strap handles and dimpled bottoms. One of these is light orange with a low straight neck and black and red geometric designs. On the sides these form two highly conventionalized monkeys whose raised faces with indented eyes project like lugs (compare fig. 22 and pl. 13, *c*).

The second vessel of this type has a low neck and more swollen body (like fig. 26). It is orange in color with a band of red and black geometric designs around the neck, a band of curvilinear designs around the shoulders, and three ornate concentric diamond designs down the body (fig. 26 had similar but more elaborate designs).

The three vessels of the fifth type, monochrome or bichrome pots with direct or slightly flaring rims and two or four vertical handles, suggest domestic or cooking ware. The largest of these has a round bottom, low lip, and four solid, vertical, loop handles. It is a dull, slightly polished red with smoke stains on the bottom. A smaller but heavier vessel is similar as to handles and base. It is lower, however, is dark red, and has more polish. The third vessel is dull buff with

vertical bands of dark red (like fig. 27). Unlike the above, it has a dimpled base and only two vertical loop handles.

A very brief analysis of other vessels reported to be from Aguacate and Aguatal, probably including some from La Ceiba as well, will bring out the major types represented here. The majority of the straight-walled vases from these sites bear Mayoid designs, very often identical with those on similar vessels from the Ulua or Sal-

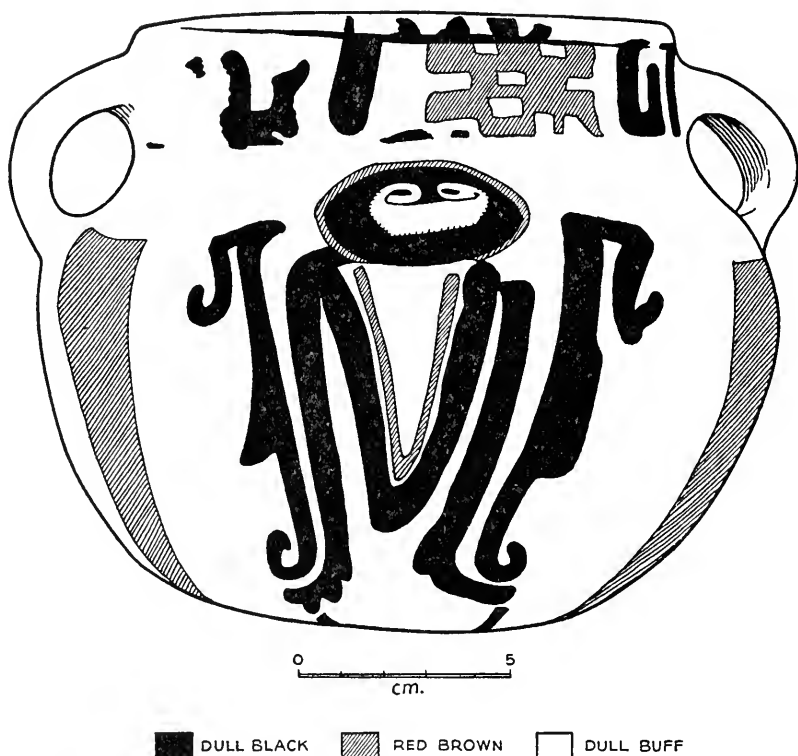


FIG. 22.—Yojoa Polychrome pot, Bold Animalistic type, Aguatal. (Specimen in the National Museum of Honduras at Tegucigalpa.)

vador regions (see pls. 12, *b*; 13, *f*, and fig. 30). Since these vases are the ones mostly highly valued by collectors, they are apt to preponderate in purchased collections, disproportionately to their actual occurrence in the field. An exceptionally fine vase of this type, said to come from Aguacate, is illustrated (fig. 30). There are three design units; two are seated priests, and the third is a monkey shown against a black medallion. The two priest designs are similar (fig. 30) except that the one not illustrated holds a five-branched scepter. This

vessel was sketched and photographed in a private collection at Jaral. The tripod dish appears to be rare, but tripod plates, with either high, hollow legs (like pl. 12, *f*) or low, hollow feet (pl. 14, *c*) containing rattles, are rather common. The majority of these have conventional designs of the Bold Animalistic type, but Mayoid designs do occur (pl. 12, *f*), including skeuomorphic glyphs and "dancing figures" associated with textile designs. Yojoa vessels of this sort appear to be somewhat more variable in size than are those from the Ulua. Small, dull brown vessels, with or without low, solid, tripod feet and decorated in the imitation Ulua marble bowl technique of incising,

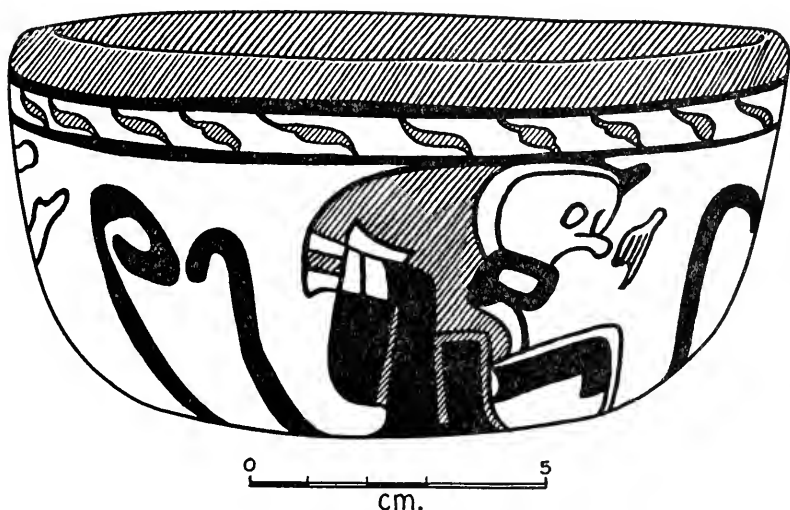
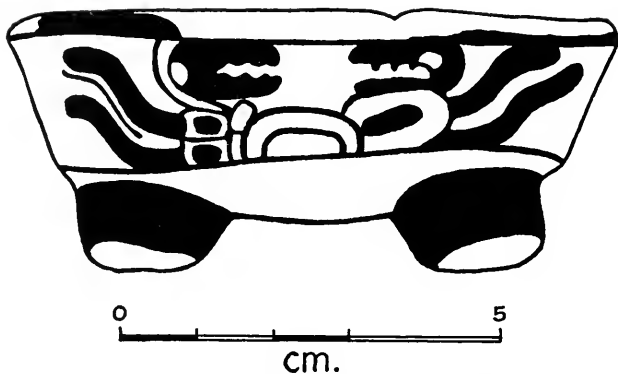


FIG. 23.—Yojoa Polychrome bowl, Bold Animalistic type, Aguacate. (Specimen in the National Museum of Honduras at Tegucigalpa.)

also occur (pl. 14, *e*). A few of these vessels, with lugs suggesting the Ulua marble bowl technique, have sculptured designs that appear more Mayoid. Particularly noteworthy at Aguacate are a few flat-bottomed dishes of highly polished dark brown ware having unique carved designs (pl. 14, *f*). These conventionalized designs are carved through the slip and, owing to the light color of the paste, stand out clearly. This seems to be a ware and decorative technique distinct from either the imitation Ulua marble vases or the Maya sculptured vessels. Open bowls vary in size and, as a rule, have two main types of design: Mayoid (often against a dark background) (pl. 12, *c*, *e*,



BLACK DESIGN ON DULL ORANGE

FIG. 24.—Yojoa Polychrome tripod dish, Bold Animalistic type, Aguacate. (Specimen in the National Museum of Honduras at Tegucigalpa.)

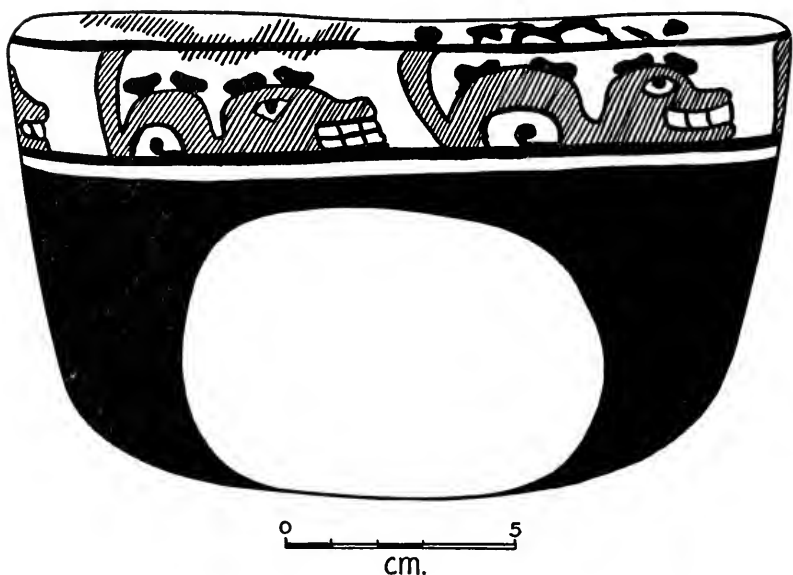


FIG. 25.—Yojoa Polychrome bowl, Bold Animalistic type, Aguacate. (Specimen in the National Museum of Honduras at Tegucigalpa.)

and figs. 28, 29); or a combination of Bold Animalistic and geometric motifs including highly conventionalized birds (pl. 14, *a, b*; figs. 21, 24), monkeys, (pl. 13, *a, b, c*, and figs. 22, 23), alligators (fig. 25), peccary, and "dancing" jaguars (pl. 12, *d*). Although somewhat similar animal motifs occur on true Maya wares, these Yojoa forms are generally distinctive and are usually associated with other designs suggesting the Bold Geometric style of the Ulua. Mon-

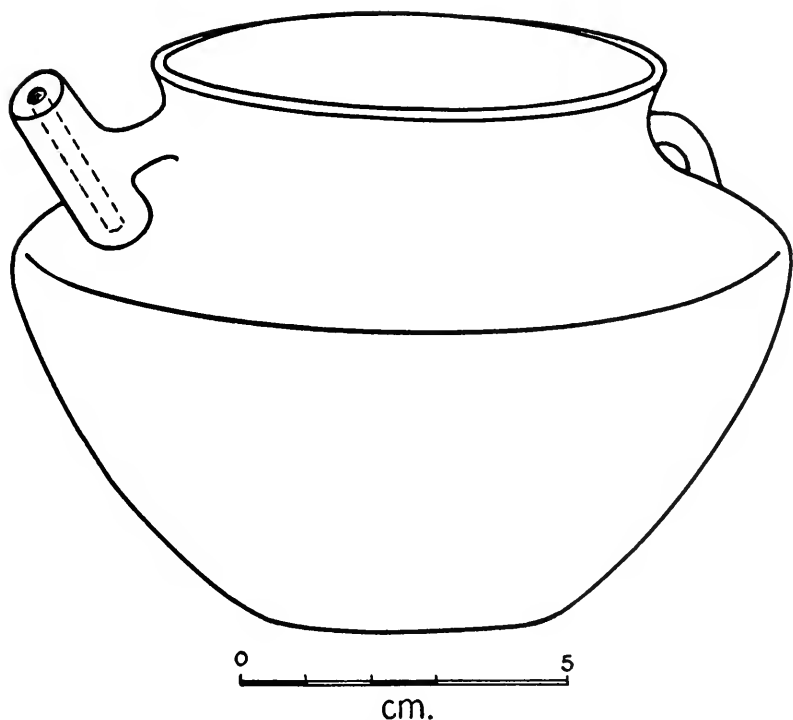


FIG. 26.—Outline of Yojoa Polychrome pot showing "vestigial" spout, Aguacate. (From a private collection at Jaral.)

key designs occur commonly on the two-handled pots with dimpled bases (pl. 13, *a, c*, and fig. 22). The range of Lake Yojoa monkey designs is extremely wide and interesting. The Bold Geometric swollen vessel with monkey lug handles is not overly common at Aguacate or other Lake Yojoa sites but does occur (pl. 14, *d*). Such Yojoa vessels are smaller than the majority of those from the Ulua and often have vestigial lugs and less striking red and black designs. These vestigial handle-lugs are also very common on the dull buff cooking vessels with dull red stripes (fig. 27). Another two-handled straight-necked

type of pot from Aguacate is decorated with intricate dark purple designs on orange. One such vessel has a panel of isolated orange heads on purple around the shoulder and an intricate purple "mask" design on the lower body and neck. The two lower design areas are separated by an ornate concentric diamond design. Figure 26 from Aguacate had a very similar design and shape except for the rather unusual but significant vestigial spout. Another vessel form, the an-

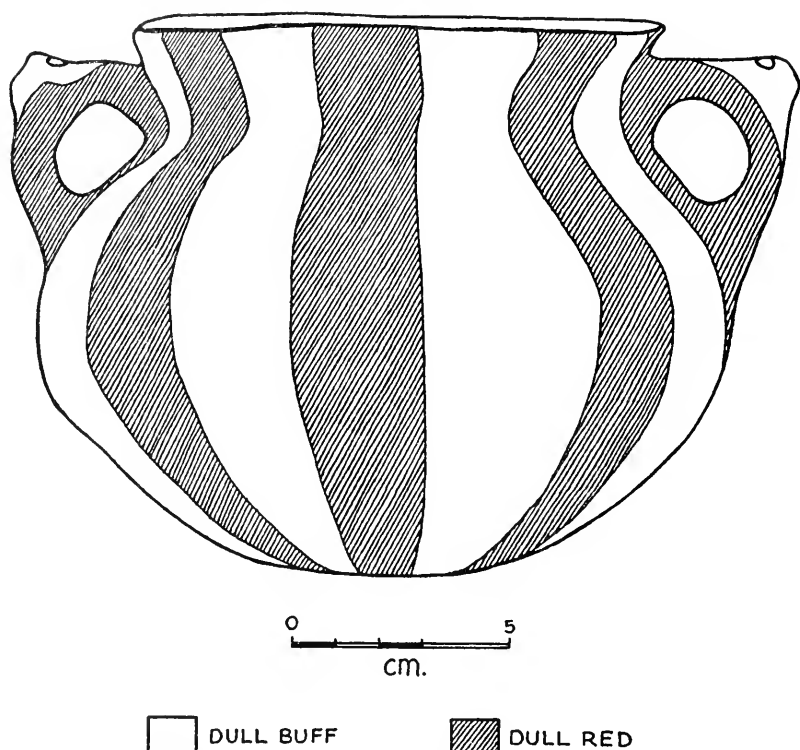


FIG. 27.—Yojoa Polychrome cooking pot, Aguatal. (Specimen in the National Museum of Honduras at Tegucigalpa.)

nular-based "salad bowl" type (pl. 14, *g*), also occurs at Aguacate. Cooking pots of dull buff color with vertical dull red stripes and two handles (fig. 27) and four-handled, polished red pots are far more common at Aguacate than any of the selected collections would indicate, for the looters usually throw these away.

No brief description can do justice to the diversity of Aguacate, Aguatal, and other Yojoa polychrome forms and decorative elements, yet it must be remembered that all of these come from the same sites

and from depths that are rarely as much as 2 meters. Moreover, despite the occurrence of at least two distinct major styles, the Mayoid and the local Animalistic or Bold Geometric, the composition and even the colors of both are similar. There is, moreover, a great overlapping of design elements. At Santa Rita (farm 17) the typical Mayoid and the Bold Geometric polychrome vessels, exclusive of the numerous intermediate types where they blend, seem more distinct than do the two major types at Lake Yojoa. Moreover, despite the great richness of color and design, the bulk of Lake Yojoa polychrome

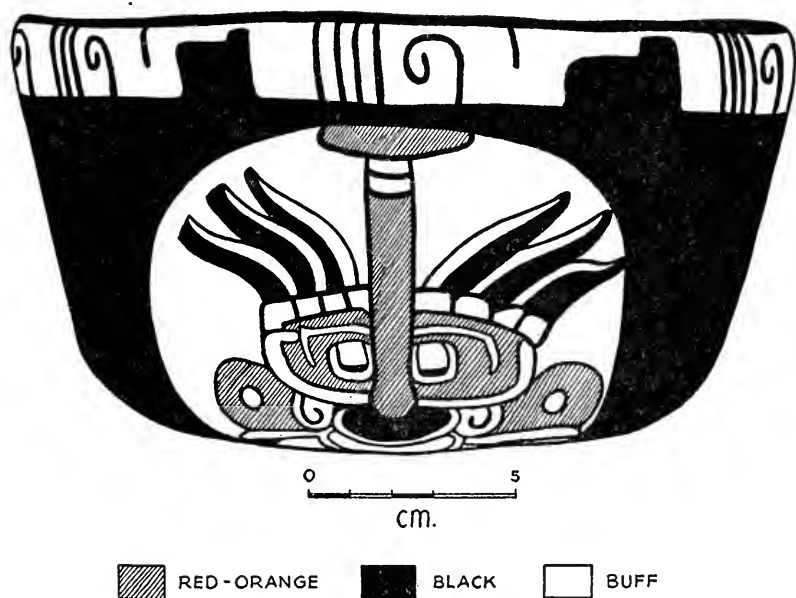


FIG. 28.—Yojoa Polychrome bowl, Mayoid type, Aguacate. (Specimen in the National Museum of Honduras at Tegucigalpa.)

pottery appears to be technically inferior to either the Mayoid or the Bold Geometric ware at Santa Rita or other old polychrome sites on the Ulua. Occasional Yojoa pieces, and these are the ones eagerly acquired by collectors, have a fine hard paste and fast colors, but for every one of these, the looters discarded or ruined hundreds of pieces that were crumbly in texture, with faded or eroded paints. Had the peoples of early polychrome times on the Ulua had the archaeological generosity to bury complete vessels with their dead, as did their contemporaries on Lake Yojoa, this comparison would be more obvious than it is at present. Analysis of paste, form, size, color, and

design, and the intercorrelation of these factors in the Aguacate-Aguatal collections must await future publication, but the foregoing, very brief, description may give some idea of their richness and the manner of their occurrence insofar as the looters have not destroyed all such evidence.

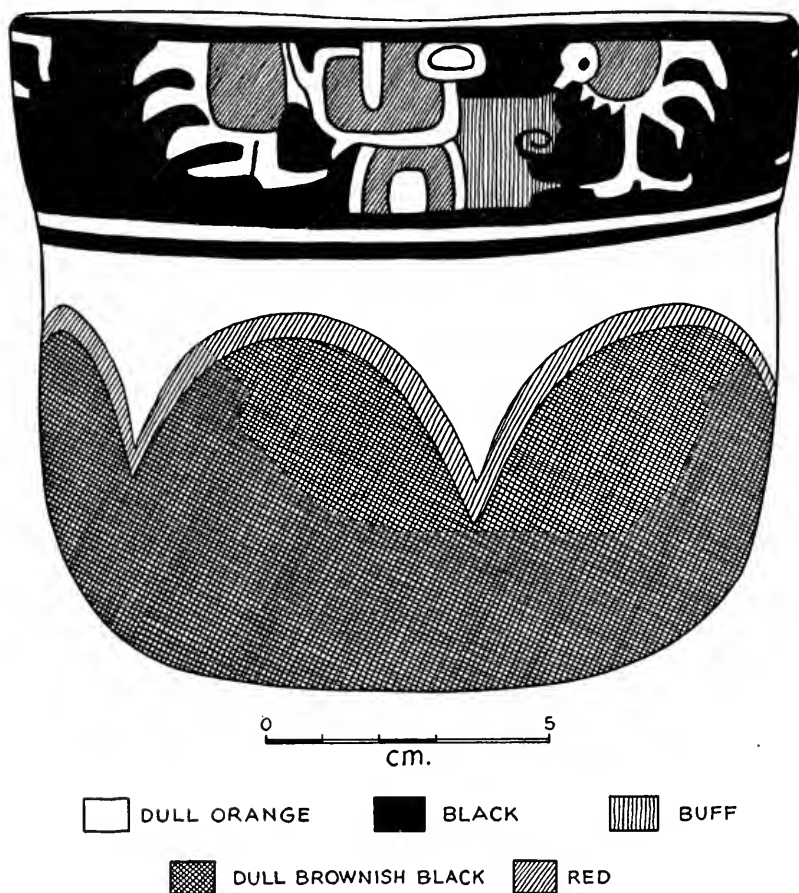


FIG. 29.—Yojoa Polychrome bowl, Mayoid (?) type, Aguacate. (Specimen in the National Museum of Honduras at Tegucigalpa.)

LA CEIBA

The first time we visited La Ceiba we walked in from Jaral by the trail to Dos Caminos and came back along the lake shore (map, fig. 20). The latter was an especially hard trip through the black mud and dense jungle of the lake shore. It was enlivened, however, by the profusion of orchids, animal tracks, and land and water birds we

encountered. Later we always rowed down in a cranky old boat, forcing our way in to shore through the massed water hyacinths (see fig. 71, Strong, 1937) to land at the old stone steps (see map, fig. 20). These roughly laid tiers of unworked stone extend several



FIG. 30.—Yojoa Polychrome vase, Mayoid type, Aguacate.
(From a private collection at Jaral.)

meters from the shore up over the barrier of volcanic rocks that lie just beyond. They appear to be artificially laid and of native origin.

SITE 1

Our first excavations were made in one of a series of low, rock-covered mounds about 1 kilometer southeast of the stone steps (site 1,

map, fig. 20). En route to the site one passes two sharp mounds about 2 meters high that have been deeply pitted by pot hunters. There are a large number of such mounds in the general vicinity. The mound selected, mound 1, when cleared, was 10.75 meters long from north to south, 10.5 meters wide from east to west, and about half a meter high. It had not been pitted. A trench 1 meter wide and 7 meters long was run from the eastern edge to just beyond the center of the mound. The soil at and above ground level was a rich black humus full of various-sized volcanic rocks. At a depth of slightly less than 1 meter below ground level, both stones and artifacts ran out, and a sterile, yellow clay was encountered. Above this, the black soil was flecked with the same yellow clay, indicating disturbance. The bulk of the sherds and charcoal occurred in the black soil below the natural ground level, the slightly raised mound area consisting mainly of rocks. No definite house floors, burials, or other structural features were encountered.

Potsherds were the most numerous artifacts from mound 1. No complete pots were encountered. The sherds were predominantly from unslipped brown cooking vessels with very heavy and solid handles which were vertical or round in cross-section. Coarse buff ware with dull red stripes and similar handles was also abundant. Polychrome sherds were few in number, mostly from dull orange bowls and tripod plates with geometric red and black designs. Legged metate fragments, fragmentary roller pestles, rectangular manos, half an ovoid sandstone bowl (1 m deep), and three prismatic flakes of obsidian were the only other artifacts. Mound 1 was apparently a habitation site judging by its contents. In all probability there were burials in the mound somewhere which led to the site having been covered with rocks, but this is problematical.

Less than a meter south of mound 1 were two small rock piles which may once have formed one mound, since the space between appeared to have been pitted long ago. An L trench which sectioned both portions revealed similar soil conditions to those in mound 1, except that the mixed earth extended to a greater depth. Artifacts were more numerous, as were also huge stones that had to be moved with crowbars. Five whole or restorable pots were found. The first, at 1.10 meters depth, was a tiny two-handled pot with its original red and black design almost entirely eroded. The second, 1.40 meters deep, was a larger, swollen-bodied red vessel with two vertical strap handles having knobs at the bend of each. A black geometric design on the neck was almost entirely eroded. Both these vessels were lying on their sides. Nearby, at a depth of 1.30 meters, was a rather high-walled,

dull orange open bowl with a simple geometric design in red around the neck. It is chiefly remarkable because it has wavy, vertical lines down the body that appeared to have been executed in negative painting. Actually, these seem to have been formed by the disappearance of the dark red paint that once covered them. A particularly interesting little tripod vase came from a depth of 1.65 meters. Like the above, it was in an upright position. This vessel has a light orange slip, two broad black lines inside and below the lip and, on the outer wall, three prancing jaguars with raised heads and open mouths, vividly executed in purplish red and black. A black and red geometric panel separates the three identical figures (the design on pl. 12, *d*, is similar but less realistic). Among the many sherds from about the depth of 1 meter we found enough fragments to restore an interesting bowl representing a bird with head, wings, and tail projecting (similar to but more elaborate than pl. 14, *h*). The basic color is light orange, and the rim, lip, bird head and tail, as well as the median portion, have dark brown, dark red, and white designs. All but the first of these vessels were broken when found, and only two were upright. It is possible that they had been placed with burials, the bones of which had disappeared, but it seems more probable that they had been discarded with the abundant sherds and other broken artifacts. Two more partially complete vessels were so soft that they crumbled to bits when we tried to remove them.

Sherds were more abundant in mound 2 and of better quality. Cooking ware was abundant and similar to that in mound 1, but there were also present a large number of fragments from large, straight-walled vases of Mayoid type. The majority of these had heavy dark red and black designs on buff or orange, with hollow rectangular or cylindrical tripod feet. A rim with a painted twilled basketry design and several with typical Ulua conventionalized heads (on thin, hard, polished ware) occur. Skeuomorphic glyph bands also occur, and there is one painted "bird" head lug. A number of excellently painted tripod dish fragments and a number of very large dark red sherds with typical Ulua Bold Geometric designs are noteworthy. These include two broad straphandles with monkey face lugs. Two figurine heads were encountered at a depth of 1.20 meters. One of these is solid, suggesting a pouting "baby face" with hair but no head dress; the other is hollow with an elaborate head dress, having a raised St. Andrew's cross above the forehead. Both are rather badly eroded. A few roller pestles, cylindrical manos, double-ended hammerstones, two crude obsidian side scrapers, one quartzite side scraper, and a few broken prismatic flakes of obsidian complete the artifact list. The

occurrence of much charcoal and small amounts of animal bone bears out the evidence of the broken pottery in suggesting that this, too, was primarily a habitation site. Our workers, accustomed to undercutting and burrowing in general, in their zeal, ruined our trench profiles at mound 2, and we decided to try another site.

Attention may be called in passing to a small collection obtained from a rock mound similar to and very close to site 1, at La Ceiba. These objects were dug up by a local pot hunter who heard us working and visited us. They included an excellent tetrapod dish (pl. 12, *f*) with conventionalized Mayoid designs, and feet representing an alligator's head and containing rattles. The colors are dark red and black on a yellow background. A small tripod dish with low, solid feet had a textile knot design with three pairs of crudely executed "dancing figures." These two vessels are of interest since they have Mayoid designs on a vessel form usually decorated in the Bold Geometric or Bold Animalistic style. One large broken whistle of unslipped brown pottery was unusually interesting since it represented a tusked monster almost identical to one found on the Uluá at Santa Rita (pl. 13, *e*, cf. fig. 7, *p*). There were also a number of Mayoid figurine and bulbous animal whistles, including howling dogs, similar to those from the Uluá. The same mound had also yielded a rectangular and an ovoid bark beater, excellently made of polished gray stone.

SITE 2

This excavation was on the southern border of the area intensively dug over 2 years earlier by J. B. Edwards. The rise or mound selected was less than 1 meter west of the remains of his headquarters shack (La Ceiba, site 2, map, fig. 20). From this point north there are a great number of irregular excavations both in mounds and in the areas between. There are numerous mounds in this immediate vicinity, and all of them are badly pitted. According to our men a very great number of pots came from this general area. The small rise or mound which we selected for work was not more than 30 centimeters high and had three irregular pot holes on its surface. It sloped slightly from the volcanic dyke on the west, extended about 18 meters to the east, and was 13 meters from north to south. Its surface was very irregular, owing to numerous volcanic rocks and to the old dirt heaps. We completed an east to west cross trench 1 meter wide through the center of the mound, but, finding that there were no regular structural details to be observed in this fashion, we carried out various extensions to the north and south. In cross-section the "mound" showed a top layer of darker soil averaging ten centimeters

in thickness. Below this was mixed brown earth containing flecks of yellow clay and innumerable large volcanic boulders. At an average depth of 80 centimeters sterile yellow clay was encountered with still more volcanic boulders, many of such great size that they could not be moved even with crowbars. Aside from various sherds and broken artifacts throughout the brown earth there were no definite floors or other evidences of artificial structure except for five groups of complete pots evidently marking graves. It proved impossible to penetrate far into the sterile clay owing to the innumerable great boulders which apparently formed part of the natural volcanic dyke.

Pottery deposit, or grave, 1 occurred just north of our cross trench on the edge of the mound. Here, at a depth of from 1 to 1.25 meters in the mixed soil just above the yellow clay and under a large number of great volcanic slabs, we found four pottery vessels (see Strong, 1937, figs. 75, 77). Three were very close together (Strong, 1937, fig. 77), and the fourth, an incense burner (not shown in the illustration), was 80 centimeters away. Three vessels were intact, but the fourth and finest (pl. 1) was broken by another bowl which had been forcibly nested in it. The broken vase, when restored, (pl. 1) was unusually interesting, since it depicted a processional group of priests calling to mind the description of Palacio (see p. 12). The first figure (pl. 1) is the high priest with the ceremonial staff; behind him is an assistant. The latter either holds a copal container or has removed the high priests' bustle with one hand and is reaching back with the other for one of the two objects carried by the third priest. These are probably incensarios, but they could possibly be obsidian mirrors or some other ceremonial objects. The three priests are followed by two musicians playing on wind instruments of an unusual type. From the attitudes of the figures, it would seem that the procession had just come to a halt prior to the performance of some rite. Further description of this vase is made unnecessary by the illustrations. The three other vessels are comparatively simple. The bowl nested in the broken vase (Strong, 1937, fig. 77 and 75, lower center) has a simple but striking black design on a cream-white background. Red and black designs occur on the lip, there is a black band inside the rim, and the under and inner slip is a dull orange. The small two-handled bowl (Strong, 1937, fig. 75, lower left) is unusually interesting since it is of the Bold Animalistic type with geometric designs around the neck, a cursive and conventionalized, twice repeated animal and circle design on the body, two handles with definite nodes on the bend, and a deep dimpled bottom. It has a bright orange slip with designs in black, dark red, and white. Thus, although the processional vase is

definitely Mayoid in form and decoration, this accompanying vessel is indubitably Bold Animalistic in type. The incensario (Strong, 1937, fig. 75, upper) is very crudely made of coarse buff pottery with dull red bands around handle and rim. From their distribution it would seem that these vessels had been laid around a skeleton, all traces of which had disappeared.

Pottery deposit, or grave, 2 occurred in our cross trench near the center of the mound at a depth of only 15 centimeters. It consisted of two vessels upright and side by side. The larger of these (pl. 13, *a*) has a bright buff slip with geometric designs in black, dark red, and bright red on neck, body, and handles. On the central body it has an extremely conventionalized monkey face with a miniature body. It is an unusually conventionalized piece of the local Lake Yojoa Bold Animalistic style. The second vessel is smaller with swollen body, slightly flaring neck, two vertical strap handles, and a small, cross-incised node on each side of its greatest diameter. It is one-color bright red and, like its companion piece, very fresh in appearance. Both vessels have dimpled bases. The larger pot contained one small ovoid bead of grayish jadeite or diorite, and the smaller pot a larger, cylindrical bead of greenish gray jadeite. The latter bead has a groove around one end and both have complete biconodont perforations. The shallowness of the deposit may indicate relative recency and the extremely conventionalized type of Bold Animalistic design on the larger vessel appears to be late (pl. 13, *a*). The fact that each vessel contained a stone bead suggests deposition with the dead, although here again all trace of human remains had disappeared.

One meter east of deposit 2 in the cross trench, at a depth of 35 centimeters, there occurred two restorable little jars of chocolate-brown ware in close association with a larger restorable pot (pottery deposit 3). One of these little straight-walled jars has three low tripod feet and is decorated with an incised diamond and dot design. The other is flat-bottomed, has two vertical lugs and a carved or sculptured design in low relief. The lugs and form strongly suggest the small pottery imitations of Ulua marble bowls, but the partially restored sculptured design seems more Mayoid. The other small jar also suggests the imitation Ulua marble bowl type (similar to pl. 14, *e*). The third restorable vessel is a typical, two-handled, local Bold Animalistic pot with a striking, heavy black and red monkey design (similar to pl. 13, *c*, and fig. 22). The broken condition of these vessels makes it uncertain whether or not they represent a grave offering. However the association of types at this depth is interesting.

Pottery deposit, or grave, 4 occurred under a mass of great rocks and consisted of three nested pots at a depth of 72 centimeters. It was located 2.5 meters east of deposit 3 in the cross trench. The upper vessel (pl. 13, *d*) was inverted over an upright, smaller, two-handled bowl, and also contained a very crude, unslipped, and slightly shoe-shaped vessel with horizontal, solid, round handles. Inside the latter was one cylindrical, thin pottery bead. The upper vessel is a striking open bowl (pl. 13, *d*) one-half of the surface of which is eroded. The original slip is dull orange, but the entire outside was covered with black, against which a thrice repeated dull orange, dark orange, and red serpent design stands out. The serpent, with bulrushlike flames darting from its nostrils, is definitely Nicoyan in style. A band of conventionalized serpent heads circle the outside of the rim and two black bands the inside. The small two-handled pot is even more eroded. It has a light orange slip, two conventionalized red and black alligator designs (similar to fig. 25) and other geometric designs on the body. The vertical strap handles have definite nodes. The coarse brown slightly shoe-shaped pot is very badly eroded and lacks all surface finish. Despite the lack of skeletal remains, this pottery deposit has all the earmarks of a funerary offering. It is particularly interesting since it contained only the local Bold Animalistic type of pottery in association with a shoe-shaped vessel.

Pottery deposit 5 consisted of several vessels uncovered in the northwest quadrant of the mound. They occurred over a triangular area 2 by 3 meters in extent and may or may not have represented one or more grave offerings. No human remains were found here or elsewhere at La Ceiba. The first vessel was a small, straight-walled bowl with a band of red frets against a brighter background around the neck. The entire middle portion of the outer body is black but much of the surface is eroded. It was found in an upright position at a depth of 45 centimeters. The next is a small, swollen pot with slightly flaring lips and small, solid, rectangular, tripod legs. It is badly eroded but has traces of black and dull buff circular designs on a dull orange background. It was found in an upright position at a depth of 30 centimeters. The third vessel is a large, badly eroded bowl found upright and wedged in among great rocks at a depth of 50 centimeters. Traces remain of an intricate but conventionalized dark red and light orange design against a black background. Like many of the Yojoa pots it has two black bands inside, below the lip. At a depth of 32 centimeters a badly eroded straight-walled vase with solid, rectangular tripod support was found upright, covered with a broken bowl. The vase had only traces of black paint on the outer

surface, but the bowl was slightly better preserved. It had an original orange slip, a band of small red horizontal chevrons outside the lip and two circular panels surrounded by a black background on the outside. The design inside these circles was gone. These vessels had evidently been broken up by roots. Nearby, at a depth of 60 centimeters, another upright bowl was encountered. It was badly eroded over its entire surface and crumbled to pieces when exposed. It seems probable that the original nature and finish of the individual pieces has more to do with their state of preservation than does their relative age or depth.

About 8 meters northeast of the mound or rise described above, and only a short distance north of the remains of Edward's "casita", was a rough stone cairn formed by about a dozen large stone slabs lying in rather orderly fashion. We commenced a trench at this point but soon ran into innumerable great boulders, laid in no particular sort of order. The trench yielded nothing but potsherds, fragments of bulbous whistles, and a few mano and metate fragments. The other mounds in this vicinity appeared to be similar to the one we cross-trenched. Many of them were higher, but all had been so badly pitted that further excavation seemed useless.

Space is lacking to describe the potsherds from these two excavations. Elaborate polychrome types were abundant, a number of Ulua types such as rows of conventionalized heads and imitation textile and basketry designs occurred; several sherds of brown engraved ware were noted; and a number of large handles having monkey faces in relief on the bend, from red-on-buff cooking vessels, closely approximate the Ulua Bold Geometric style. A few heavy, coarse sherds with rough incisions suggest graters, and a number of ground-down disks of polychrome pottery occur. The more localized Yojoa Animalistic and Mayoid polychrome types are generally the same as those described in the complete vessels and in the Aguacate ceramic material. Complete figurines are lacking, but a brown ware fragment, from a depth of 30 centimeters, depicts a woman's breasts supported by a bar or pendant as in certain Maya stone sculptures. A few bulbous bird and animal whistle fragments are present. Heavy volcanic stone metates, both with and without tripod supports, were fairly numerous, and both roller pestles and small rectangular manos occur. An ovoid wedge or chisel, 10 centimeters in length, of hard gray-green stone is interesting. From a depth of 20 centimeters comes a flat slab of hard gray stone with a sharp, ground-down edge. Numerous prismatic flakes of obsidian, a few crude obsidian and flint side scrapers, and some red ochre, were also found. Round stone balls were fairly

numerous at the site. The occurrence of two jadeite beads has already been noted. On the whole, nonceramic artifacts are more abundant in Lake Yojoa than in Ulua Polychrome sites.

SITE 3

About one-third of a kilometer north of site 2 we briefly investigated what appears to be a quite different type of mound. To reach it one proceeds through the extremely dense bush past a great number of low, pitted, rock mounds (La Ceiba, site 3, map, fig. 20). Despite its relative proximity to the lake we doubt if we could have found it without the aid of Paco. The mound in question we called the "cut-stone mound", because of the occurrence there of several large slabs which appeared to have been worked. The main structure is a rectangular platform-mound, 2.80 meters in height, with a north to south length of about 20 meters, and a breadth of approximately 10 meters. The walls of this mound rise sharply, and the top, which measures roughly 14 by 6 meters, is rather flat. The south end, which faces the lake, has a more gradual slope, but the north end and east and west sides rise abruptly. This platform-mound is set upon a low circular rise, or mound, which has an estimated diameter of almost 40 meters. It was impossible to clear this entire area with the time and men available; hence these measurements are merely approximations.

An excavation had been made near the center of the platform-mound which reached down to subsoil, a depth of exactly 2.80 meters. When cleared, the walls of this pit proved to be of brown soil containing, especially near the bottom, some potsherds and charcoal. The very bottom of the pit reached sterile yellow clay. No large rocks occurred in the walls of the pit, but we found a few just under the surface elsewhere on the platform. The local man who had dug the pit told us that he had found nothing. To the south, where the platform-mound rises from the low irregular substructure, we encountered a row of boulders which seemed to form a lower border. Ten meters farther south, still on the sloping substructure, we uncovered a number of large, flat slabs, several of which appeared to have been more or less ground into shape. These were immediately adjacent to an old excavation containing other slightly worked, flat slabs. Our workers told us that four small pots had been found in this pit. Aside from being laid flat, none of these large slabs appeared to be in any particular arrangement. Two meters farther south on the outer edge of the substructure, we encountered a row of boulders and smoothed slabs laid end to end just under the surface. These slabs and boulders formed a definite border to the substructure

which we followed for 8 meters, paralleling the south face of the inner platform-mound.

Approximately 20 meters south of the "cut-stone mound" is another, lower mound and, running west-northwest of this, is a row of regularly aligned boulders barely projecting above the surface of the ground. These extend for about 20 meters and then take a 90°-turn to the south. We lacked time for further investigation, but it is apparent that both the "cut-stone mound" and its neighbors represent a structural unit of some sort, the nature of which may only be determined by adequate clearing and excavation. The rough boulder and slab structures are similar to those at Agua Azul, to be mentioned later. Similarly, we encountered very few polychrome sherds in our brief work around the "cut-stone mound", the majority being of coarse, plain ware.

CAUSEWAY AND "CANAL" NEAR JARAL

With the exception of the concentration of burial and other mounds near Aguacate and La Ceiba, the great bush-covered plain east of the Jaral-Potrerillos road appears to be without noticeable archeological sites. At present this is the area where most of the scattered milpa farming takes place, the soil being reported as very fertile. Just to the east of this road we discovered a great causeway and "canal" which separates the ancient ceremonial center near Los Naranjos from the main agricultural area and the burial sites farther to the east (see map, fig. 20). Following up local stories of "an ancient canal to drain the lake", we visited El Eden and found that the story had a basis in fact (Strong, 1937, fig. 73). Later, guided by Miguel, we followed the entire length of this structure from where it enters the lake to its northeastern termination on the Rio Blanco (map, fig. 20), an estimated distance of 5 kilometers. With the exception of perhaps 300 meters at El Eden which are cleared, the remainder of the structure is covered with dense bush, and we had to cut our way through. It took us about 5 hours to make the trip.

The structure, which appears to be continuous, consists of a large, flat-topped causeway on the west, bordered by a definite borrow-pit or "canal" on the east. It enters the lake about one half a kilometer east of Jaral. Here the borrow-pit is 25 meters wide and the mound to the west about 8 meters wide and .75 meter high. To the east of the borrow-pit is a rise of about 1 meter. Where the mound crosses the trail from Jaral to Dos Caminos (map, fig. 20) it is about 14 meters wide and 2-3 meters in height. The ditch is not visible at this point. About three-fourths of a kilometer farther north the mound is 5

meters across and 4 meters high. The borrow-pit or ditch is 25 to 30 meters wide and is flanked by high ground to the east. At El Eden, where it crosses the road to the cemetery, the mound is 21 meters wide, 3.5 to 4 meters high on the ditch side, and 2-3 meters high on the west side. The ditch here is 9 meters wide across the bottom. About 100 meters north of this road is an apparently intentional break in the mound wall about 16 meters wide (Strong, 1937, fig. 73). About 22 meters farther on is another smaller break, perhaps worn through by an old road. With these exceptions the mound or causeway appears to be continuous throughout its entire length, though the poor visibility due to the dense bush prevented our perceiving all details as we cut our way through. About half a kilometer north of El Eden the mound, now definitely turned to the west, crosses the road, where it shows in cross-section on the east side. The ditch here is not marked. Beyond the road both mound and ditch again become very definite with fairly steep walls. Here, as elsewhere, the mound has a flat top. Both terminate in a series of mysterious, deep, dry gorges which mark the underground course of the Rio Blanco. Miguel pointed out another series of deep pits or small gorges just south of here extending to the west (map, fig. 20), which he said marked the course of another underground stream called the Jutosa. At the time of our visit (April 4) no water was visible in either stream at this point, but during certain seasons the water level is said to rise to a considerable height.

It is certain that any clear understanding of the function of this interesting causeway and "canal" will depend on an equally clear understanding of the nature and recent history of these mysterious, semisubterranean streams. Hidden amidst almost impenetrable bush and marked by precipitous canyons and yawning sink-holes, the solution of the problem of the Rio Blanco, which apparently drains Lake Yojoa by some subterranean passage, is not one to be lightly attempted. There is probably some connection between the past level of this stream and the "canal" in question. If the river level was at one time higher than at present, the "canal" would have served to irrigate a large portion of the lower plain. Strange to say, local tradition reverses this explanation and claims that the ancient Indians sought to drain the lake! Since returning to Washington, the senior author has also heard a story that a canal was dug in this vicinity about 1880 by a commercial company with some similar end in view. We have as yet been unable to secure more definite information in this regard. We are unable to state positively that the causeway and ditch are not of historic origin, but, to say the least, this seems highly improbable.

From the slope of the terrain we would estimate that the northern end of the "canal" is at least 50 to 60 feet higher than its southern termination on the lake shore, hence any attempt to "drain the lake" would be absurd. This same factor, however, would favor the theory of a great central irrigation ditch, should geologists determine that the water level of the Rio Blanco was once considerably higher than at present.

There is another possible explanation which emphasizes the continuous mound or causeway and accounts for the ditch or "canal" as merely a borrow-pit. A glance at the sketch-map (fig. 20) will show that the causeway might well have been a ceremonial or defensive structure enclosing the great mound group west of Jaral, since it extends from the steep, encircling mountains all the way to the lake. A flat area is thus entirely enclosed and in the center of this rise the great mounds of Los Naranjos (fig. 20). Here we must leave the problem, the true answer to which must depend on the cartographer, the geologist, and the adequate excavation of the archeologist.

PYRAMIDS AND STONE STATUES NEAR LOS NARANJOS

The dominant archeological feature on the north shore of Lake Yojoa is the extremely impressive group of great mounds, or pyramids, located about 20 minutes' easy walk west of Jaral (see map, fig. 20). This site was first described by Mrs. Doris Zemurray Stone (1934) as the southernmost known Maya city and designated Los Naranjos, after the little modern village to the west. J. B. Edwards has made what appears to be an excellent sketch map of this site based on his own explorations. He very kindly furnished us with a copy of this. So far as our own sketch map (fig. 20) is concerned, we have located and numbered these mounds in general accordance with Mr. Edwards' map, omitting, however, mounds 6 and 7, slightly east of the main group, which we did not examine ourselves. Since the Los Naranjos mounds or pyramids cover a large area and are all covered with dense forest or bush, the preparation of an accurate, surveyed map would be a considerable task. Until this is accomplished Mr. Edwards' map is the best available and, so far as our own limited explorations went, seems generally accurate. We have not reproduced it here, however, since it was primarily made for Frans Blom and will probably appear in connection with publications of Tulane University.

The Los Naranjos mounds or pyramids are of great size, as indicated by our photograph of one of the smaller terraced mounds (mound 1, pl. 16, fig. 4). Yde has overdone it, however, when he shows

a photograph (1935, fig. 4) of the sharp, natural hills behind Los Naranjos with the caption, "View of the Mounds at Jaral." His photograph, probably taken from mound 1 (pl. 16, fig. 4), overlooks the great mounds to the south which, however, are shrouded in jungle and do not show in the picture. As a result, the reader might easily assume that the natural hills which do show are the pyramids. Perhaps the translation should have been "View over the Pyramids", rather than "View of the Pyramids." Mound 1, (pl. 16, fig. 4) appears to be terraced, and we estimated its height at some 6 meters. Mound 4 (fig. 20) is much larger and higher, perhaps 8 to 10 meters. It is terraced and has a number of smaller mounds forming a court on the top. There has been considerable digging here, probably by road workers seeking paving stones, as well as by pot hunters. Sherds seemed to be scarce on the surface. The other mounds appear to be smaller than mound 4, but several of them are terraced and all are worthy of careful mapping and investigation. Owing to the dense bush, it is impossible to make adequate observations without a great deal of clearing. Since we lacked facilities for this type of work or for any large scale excavation, we limited our own activities to smaller sites on the norther border of the great group (site 1, Los Naranjos, map, fig. 20).

The occurrence of a number of fragmentary stone statues at the Los Naranjos site is particularly interesting (Stone, 1934; Yde, 1935 and 1936; and Strong, 1937). These have all been removed from their original sites, probably by road workers, who have undoubtedly broken up and carried off others. Those which we located were lying in the great plaza between the Los Naranjos mounds at three places near the Jaral-Los Naranjos trail (map, fig. 20). Probably these had once been placed on top of mound 4, or one of its neighbors, and later tumbled down by the road workers. One statue represents the body of a man or ape, with one hand resting on the hip, the other crossing the body and resting on the shoulder (pl. 16, fig. 3). Feet, arms, and the head had all been broken off long ago. The material is a hard, gray, volcanic stone, and the body at present is 1 meter high and 50 centimeters wide across the shoulders. The neck break at present measures 23.5 centimeters from front to back. The body has a primitive simplicity and grace despite its solidity. Aside from two parallel incised lines on the back, suggesting a belt, there are no other notable features. Mrs. Stone describes a similar mutilated figure with a string of beads around the neck (1934, p. 126); hence there must be at least two of these figures. Next to this stone body was a large grotesque head (pl. 16, fig. 3) which evidently belongs to the body,

although the uniform patination indicates that the original break occurred long ago. On the head the outline of breakage at the neck is very similar to that on the body. It measures 22.5 centimeters from front to back. The apelike head is disproportionately large for the body and distinctively prognathous. Anthropomorphic characteristics are the elongated and, presumably, decorated ears and a row of incised circles down the back of the head. Next to the other anthropomorphic torso with beads around the neck described by Mrs. Stone (1934, p. 126) there was a similar head. We would be inclined to regard this as identical with the one here figured (pl. 16, fig. 3), but Mrs. Stone does not mention the macrocephaly, which is so outstanding in the head here figured, and states that it had circular ear plugs. From her description of it as "thick lipped" and "soft nosed" with eroded features, the two, if not the same object, must have been similar. We saw only one head and Yde and his party none.

Mrs. Stone (1934, p. 126) calls the anthropomorphic statue a "stela", and stresses the position of the hands as representing "without a question of doubt, the Mayan sign for submission." Yde (1936, figs. 3, 4, and pp. 27-29) also figures this statue and apparently concurs with the interpretation of Mrs. Stone. In our opinion, neither the body nor the head are Mayan. Rather they appear to us as closely related to that widespread, and probably older, "Chorotegan" style of stone statue which occurs commonly in Costa Rica, Nicaragua, the highlands of Guatemala, and, rarely, on the Ulua (Lothrop, 1921). The archaic simplicity of the torso, plus the crudity and simian characteristics of the head, seem totally non-Mayan in feeling and technique. The position of the hands alone suggests a definite Maya convention, which may be relatively early but was certainly in vogue at a late period at Chichen Itza (see Tozzer, 1930, pp. 155-158). However, the same position of the arms, as well as crossed arms with the hands on the shoulders, occurs on a number of simian stone statues from Costa Rica, now in the United States National Museum. These statues, and others figured by Lothrop (1921) seem much closer to the Lake Yojoa stone figures than do the highly ornamented and definitely stylized Mayan bas reliefs or vase paintings. If the coincidence of hand position is not accidental in regard to the two types, it may well have some historic significance. The relationship of the Lake Yojoa stone carvings to the southern, "Chorotegan", type is even more forcibly demonstrated by another anthropomorphic, cylindrical, stone carving from Los Naranjos (pl. 16, fig. 1, and Yde, 1936, fig. 6). This type is identical with the rather common, anthropo-

morphic, giant "roller pestles" of northeastern Honduras (Strong, 1935, p. 148).

With the anthropomorphic head and body, we also found the stone serpent head (pl. 16, fig. 2) referred to by Mrs. Stone (1934, p. 126) and Yde (1936, p. 29). By some strange mistake, Yde (1936, fig. 28) figures a side view of the "submissive figure" which he designates as the serpent's head. This piece is 80 centimeters long and 37 centimeters wide across the broken base. It, too, is of hard gray volcanic stone. A short distance west of mound 4, we noted a cylindrical stone, 95 centimeters long, smooth on one end and broken on the other, which apparently had once formed the base of the serpent head. It would be interesting to know whether the stone serpent on the "Islita", mentioned by Yde (1936, p. 30), was of the same type. He refers to a photograph of it in his article (1936, p. 30), but there is none. The style of this Los Naranjos serpent head carving (pl. 16, fig. 2) is very well executed and distinctive, but we cannot definitely place it. It would be extremely interesting to know whether it pertains to the same period as do the anthropomorphic statues.

We did not see the various, undecorated, great stone slabs described and figured as "stelae" and "altars" by Mrs. Stone (1934, p. 127) and Yde (1936, p. 29, fig. 5). In the light of general distribution, however, we would be prone to relate these to similar erect stone slabs at Plan Grande in the Bay Islands and elsewhere on the mainland of northeastern Honduras (compare Strong, 1935, pl. 33 and pp. 160, 161) rather than to true hieroglyphic stelae of the Maya. As Yde (1936, p. 29) points out, the flat rock with irregular carved grooves on its surface in the plaza of Los Naranjos is very similar to others occurring at Tenampua (compare D. H. Popenoe, 1936, pl. 5, fig. 1). The adjacent flat rock with depressions suggesting three shallow bed-rock mortars seems more unique in this area. In a later report, it will be possible to publish adequate photographs of these interesting statues and carvings, but this cannot be done here. When the great site of Los Naranjos has been cleared, and excavations on a scale worthy of its size and importance have been commenced, more statues will undoubtedly come to light. It should then be possible to correlate them with their exact cultural horizons and thus end the unsatisfactory speculation which must always center about disassociated art objects.

EXCAVATIONS ON THE NORTHERN BORDER OF LOS NARANJOS

Just north of mound 1 is a bushy field where a considerable amount of digging has been done in the last 3 years. We chose this place for

work because Mr. Edwards reported deep, and possibly stratified, burials here, and M. K. Rittenhouse reported the finding of two pots of the old Playa de los Muertos type (pl. 15, *a, b*) amidst similar sherds at a depth of less than a meter. The surface of the field was irregular, but definite mounds were hard to find in the dense, low bush. However, ticks of all sorts were not. We selected and cleared a roughly circular mound, 18 meters wide from north to south, 21 meters wide, and 50 centimeters high, located about 100 meters north of the western end of mound 1 (map, fig. 20). East of the center line of the mound we dug a north-to-south trench 2 meters wide and 12 meters long. The west wall of the trench was later extended 3.5 meters north, and two western side trenches were dug well beyond the center of the mound.

A small portion of the long western wall of this cut is shown (pl. 16, fig. 5, and text fig. 31). A layer of dark, humous soil occurred just below the surface on the entire mound (fig. 31). Just below this, in the thick deposit of yellow-brown mixed soil we cross-sectioned the entire floor of a house (see house floor, fig. 31) composed of black, burned soil containing many sherds, metate fragments, and refuse. Beyond the edge of the diagram here shown (fig. 31), this occupation level or floor dipped, forming a level area for about 5 meters, then rose to the ground level, extending on into what appeared to be another floor or occupation level beyond the limits of the excavation. The same type of occupation level also occurred at the surface on the south end of our main trench. Our western cross trenches showed that the central floor area extended 2 meters to the west, where it again rose to the surface. No post holes occurred in our cross-section of the central house, but one was found extending below the occupation level at the north end of the central trench. No special fireplaces were noted, but charcoal was abundant. Judging from our trenches, there are numerous house floors in this vicinity, on or just below the present level of the ground. These contain the finest Yojoa polychrome and associated cooking ware sherds, along with other refuse. Here, as at Naco, an expedition engaged in other than exploratory, stratigraphic work, could easily clear entire house floors and work out the features in detail. During the first part of our work the trenches were taken down below the occupation area into the sterile, yellow clay and gravel stratum (fig. 31) which occurred at an average depth of about 1.3 meters below the surface. Polychrome sherds, stones, charcoal, burned clay, fragments of pumice, and broken artifacts occurred throughout the yellow-brown soil. The mixed soil level became darker just above the sterile layer (pl. 16, fig. 5, and text fig.

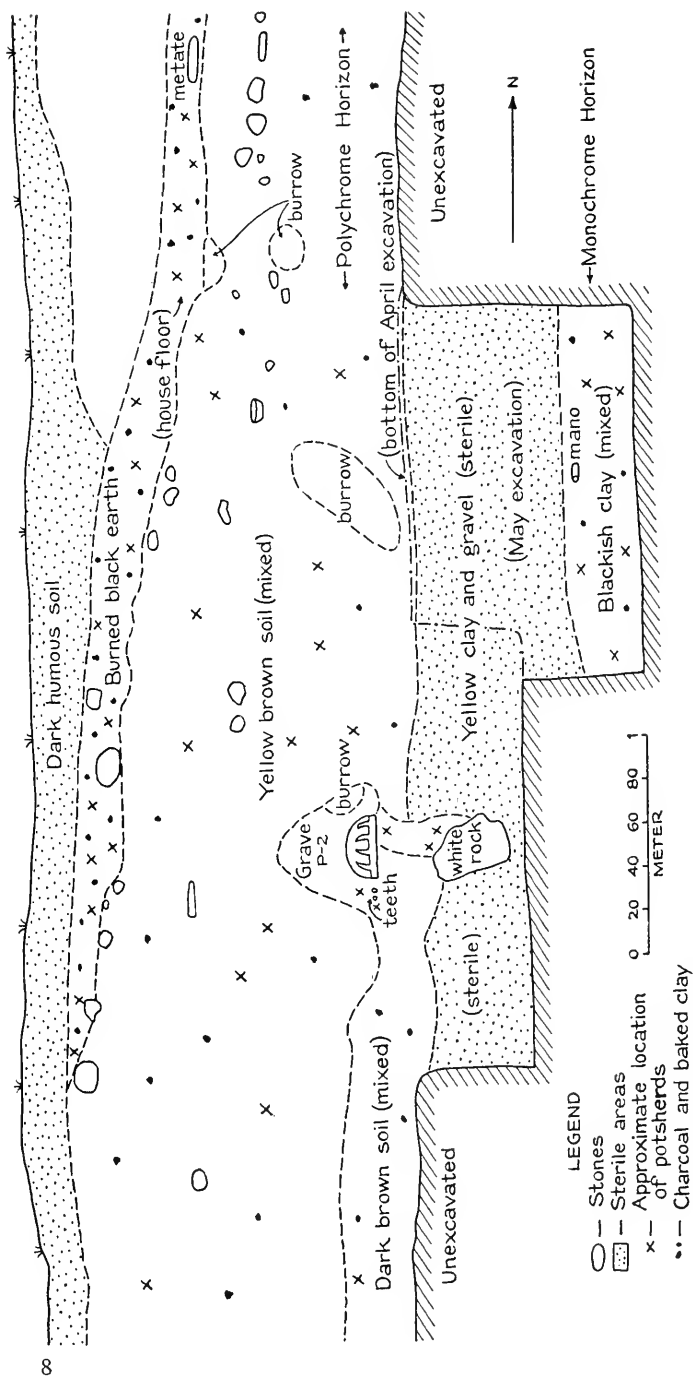


FIG. 31.—Cross-section of west wall, site 1, Los Naranjos, showing house floor, burial, and superimposed cultural horizons.

31). Below the house floors, or occupation levels, we encountered several burials (see P 2, fig. 31) of the polychrome period. For the present we will confine ourselves to a brief discussion of features and artifacts from this upper or polychrome level, later discussing the materials below the sterile stratum. All vessels and important artifacts were photographed *in situ*, but these, like our complete cross-sections and ground plans, cannot be presented here.

At the extreme south end of the main trench, at a depth of 94 centimeters, we found a small orange bowl decorated with crude red alligators and black scrolls. It was tipped on one side. No bones were present. A deposit of three vessels occurred near the north end of the main trench at a depth of 1 meter. There were two superimposed bowls, one with a cream-white slip on which were three dark red and orange designs of Mayoid type, probably conventionalized serpents' heads; the other was orange with a much conventionalized, seated Mayoid figure. These two bowls were inverted. Next to them was an upright, small, but striking, effigy bowl, modeled to represent a frog. It was brown and unslipped. This was probably a grave, occurring at the base of a refuse heap. However, no bone was found. About 2.50 meters from the south end of the trench near the west wall, at a depth of 1.45 meters, we found an interesting upright bowl (pl. 14, *d*). This was small but of the typical Santa Rita Bold Geometric olla shape and color (compare pl. 14, *d*, and pl. 7, *a*). The present vessel has the same light orange slip, with similar red semi-circles inside the lips as do the monkey-handled ollas, but the geometric and conventionalized designs are in dull red with no black. The base has the marked dimple, and the handles have the lugs of the Ulua Bold Geometric olla type.

Slightly north of this pot, at the junction of one of the western cross trenches, five vessels were uncovered at depths of from 1 to 1.45 meters. This immediate area had been badly disturbed by armadillo burrowings (see grave P 2, fig. 30, and pl. 16, fig. 5), but all the vessels were evidently part of one grave offering. In between them were found a few small, crumbling fragments of human bone and three caps from human molar teeth, thus proving for the first time the presence of a burial. As can be seen from the photograph (pl. 16, fig. 5) and diagram (fig. 30) this burial occurred under the southern edge of a house floor. Only one vessel shows in the cross-section diagram, the others being just east of the trench wall. This bowl was inverted. It was fluted and had a splotchy, light orange slip, with crude red linear and geometric designs. On the inside a slightly darker orange wash has been added, leaving thin vertical

stripes of the lighter slip, thus suggesting negative painting. The bowl is blackened by fire on one side of the bottom, suggesting that, despite its thinness and fine, hard paste, it might have been used for cooking. Just east of this vessel, at a depth of 1 meter, was a crumbly red bowl containing a fragile little tripod vase with black and red decorations. Both these vessels, despite our greatest care, crumbled into tiny fragments when removed. At a depth of 1.45 meters, 30 centimeters to the south of these, was an upright incensario containing a considerable amount of charcoal. It had nine perforations and a solid, rectangular handle which had been completely hollowed out from the top. The incensario had a dirty, cream-colored slip, with both upper and lower edges outlined in red. The fifth bowl (pl. 13, *b*) was slightly to the north, at a depth of 1.45 meters, in an upright position. It has an orange slip, with a band of white below the rim and three white bands down the sides, dividing the outer surfaces into three panels (pl. 13, *b*). On the white bands are unusual geometric and curvilinear designs in dark red and, on the sides, orange. In each of the three panels occurs a most interesting prancing monkey, done in dark red. The bottom of the bowl is flat.

In the south wall of the southerly, east to west extension trench, at a depth of 64 centimeters, was an upright, two-handled, cooking pot, 22 centimeters high and of a dull yellow color. Inside this large vessel was an inverted polychrome bowl with a yellow slip, a row of red conventionalized Mayoid designs outside the lip, and three big black circles on the sides. The designs were badly eroded, but the bowl was intact. The outer vessel barely held together while being uncovered and photographed, but the moment we touched it, to remove it, it fell into over a hundred small pieces. Close to these two vessels was a dull cylindrical stone bead. On the north wall of the other extension trench, 1.25 meters deep, occurred a small open bowl of rough gray unslipped ware. At a depth of about 1 meter, near the west wall of the main trench, we found restorable fragments of a vertical walled vase with solid, rectangular tripod feet. It has a rich orange slip, divided into three parts on the sides by dark red and black linear designs. Red and black lines circle top and bottom, and each panel contains a well-executed seated Mayoid figure, with elaborate headdress, bustle, and outstretched hand, done with fine lines. Later, when this site was reopened to dig through the sterile layer searching for deeper cultural material, a small "salad bowl" type vessel (pl. 14, *g*) with an annular base, was found nearby right side up at a depth of 1.10 meters. This bowl is interesting because of its shape and because of the darker orange wash through which

horizontal and vertical lines of the lighter underslip stand out. More complicated curvilinear designs of this type occur on the inside of the bowl. This rather peculiar type of negative painting is well shown in the photograph (pl. 14, *g*).

The foregoing account, in conjunction with that of our excavations at La Ceiba, gives an idea of the manner in which vessels representing the various types of polychrome ware occur in the smaller Lake Yojoa mounds. Later, in connection with a site at El Eden, we will discuss the present slender evidence regarding the apparent vertical distribution of Yojoa polychrome pottery types in these relatively shallow sites. Although traces of human bones occurred with only one of our burials, there seems good reason to believe that the majority of these pottery caches were once with skeletons, all traces of which have now disappeared. It is further indicated that these low mounds also served as places of habitation during the polychrome period, and that burials occurred beneath the house floors. Probably, as at La Ceiba and Aguacate, many of these mounds were used, or came to be used, almost entirely for burial purposes, and it is in these that the great masses of rocks occur. Others, like the site we are discussing, served primarily for habitation, but burials also took place under and near the houses. Such habitation mounds seem to have relatively few large rocks. There remains briefly to sketch in the rest of the artifact content of the polychrome horizon at this site, and then to describe the occurrence of a deeper, older, cultural horizon which was encountered at the very end of our stay at Jaral.

The sherds from this one Los Naranjos mound site present a wide variety of Yojoa polychrome types. In addition to those already mentioned among the entire vessels are Mayoid pieces with incising as well as painting; Bold Animalistic sherds; heavy Bold Geometric sherds; polished brown carved fragments; heavy gray or buff sherds painted only on the flat upper surface with bright black, red, and orange designs (one of these is flat with a small annular base); unslipped brown grater fragments; and two cylindrical spouts of coarse brown pottery. The latter may have been carried in by the natives from older deposits since we have seen no Lake Yojoa polychrome vessels with this type of spout. One candelario fragment of coarse brown ware has three compartments and simple incised designs. There are two spindle whorls, one of plain brown ware, the other a ground-down, painted sherd. All the above come from depths ranging from the surface to 1.45 meters in depth. A complete Mayoid figure forming a whistle comes from a depth of 65 centimeters, and a bird whistle from 1.10 meters. In addition, there are numerous fragments includ-

ing broken but ornate, hollow, Mayoid effigies of fairly large size. Figurines are varied. Solid and hollow figurines with square Mayoid headdresses (like fig. 7, *b, i, s*; also see Gordon, 1898, pl. 9, *l, n, v, s*), as well as solid heads with pouting faces and simpler hair dresses, all come from depths of 1 to 1.45 meters. This latter type of simple, well modeled, solid figurine also occurs in polychrome deposits on the Ulua. Several of the Los Naranjos figurines are extremely crude, solid lumps of baked clay with grotesque, punctate faces or filleted "coffee-bean" eyes. These have a decided "Archaic" appearance but occur in the same horizon with the polychrome pottery and ornate figurines. In addition to the figurines this deposit yielded a considerable number of filleted or modeled fragments of baked clay. Many of these are quite complex but their original form is uncertain. Ground stone artifacts are fairly abundant, including flat ovoid lapstones; both flat and tripod rectangular metates (the majority with a broad grinding groove); cylindrical roller pestles (including some that taper at both ends); hammerstones; one small rock mortar; two small, sharp, jadeite celts (1-1.10 m deep); and one brown stone bead. Chipped stone artifacts are simple but relatively abundant. Large and small, fragmentary, prismatic flakes of obsidian occur. There are numbers of crude obsidian flakes, evidently used as scrapers, and a few flakes of other stone. At a depth of 1.10 meters we found the only definite projectile point encountered, a planoconvex, obsidian dart point with a slight, tapering stem. Even this brief summary indicates that these small Lake Yojoa sites are far more prolific in nonceramic artifacts than are sites on the Ulua or the Chamelecon Rivers.

THE OLDER HORIZON AT LOS NARANJOS

Our main work at Lake Yojoa was terminated by the advent of "Holy Week." It was then necessary to move on to Playa de los Muertos on the Ulua, and then to Naco if we were to complete the survey we had outlined. We had determined the general association of polychrome wares at Lake Yojoa but had not found any marked stratification of cultures, nor had we encountered the old type of Playa de los Muertos ware (pl. 15, *a, b*) discovered in the vicinity of Los Naranjos by Mr. Rittenhouse. Despite his statement that it had been found here at depths of less than a meter, we had so far been unsuccessful in locating any remains other than those of the polychrome period. It was obviously necessary to go deeper and penetrate below the sterile yellow clay stratum encountered at our Los Naranjos site.

Therefore, in May, when the rest of the expedition went to Naco, Mr. Paul returned to Jaral for this purpose. Efforts to locate the

exact Rittenhouse site through his former workmen again proved unsuccessful. Mr. Paul therefore sank a small test trench (B) 6 meters southwest of the mound we had excavated (fig. 20). Passing through the polychrome horizon, which was removed in 30-centimeter levels, he again encountered the sterile layer of yellow clay and gravel which here averaged about 50 centimeters in thickness. Digging through this, he encountered a brownish black clay which contained a small amount of cultural admixture. All potsherds from this lower occupation level proved to be of a crude, monochrome type. This lower cultural horizon averaged about 65 centimeters in thickness, dipping toward the east end of the trench, and terminating in a very hard yellow clay which appeared to be absolutely sterile. To check these results he dug another test pit (A) 8 meters to the southeast of the same mound. Here he again encountered the same soil and cultural conditions (fig. 32), the brownish black clay below the sterile clay yielding only coarse monochrome potsherds and a few other artifacts. He then returned to our former excavation and sank a pit next to our old test cut into the sterile stratum (fig. 31). Only 25 centimeters below the lowest level of our former excavation he ran through this sterile layer into the darker clay, obtaining monochrome potsherds and a small mano. It is evident, therefore, that this direct superimposition of two cultural horizons, separated by a sterile stratum of yellow clay and gravel, extends over a considerable area. The same strata vary slightly in thickness and absolute level at the different pits (compare figs. 31 and 32), but the sequence is the same in all. Material from the lower cultural horizon is likewise uniform and may be discussed as a unit.

The deeper ceramic remains, some 700 sherds, are extremely crude (pl. 15, *c-w*). They are all of a crumbling ware, tempered with finely ground stone or sand. The apparent similarity in texture between this older ware and the poorer grade of Yojoa Polychrome, especially the cooking ware, suggests that both were made of inferior, local clays. This point may be determined later by microscopic analysis. All sherds from the old horizon seem to have come from small vessels. The thickest sherd is 1.4 centimeters, the thinnest .4 centimeter, and the majority average about .7 centimeter. Some are badly waterworn (pl. 15, *r*), and the majority have one or both faces considerably eroded. Of the 51 rim sherds, the great majority have low, slightly flaring lips (pl. 15, *c, d, f, g*). A small proportion of lips are swollen, and there are a few vertical and a few direct rims. Two sherds from the same vessel, seem to be parts of an annular base, but the remaining 30 basal sherds are all from small, flat-bottomed vessels (pl. 15 *s, u, v, w*). There are no spouts, handles, lugs, or feet in the present

sample. Only 12 sherds show definite traces of slip or paint. The others range in color from a dull buff, through dull red, to a grayish black. Despite the obvious erosion on many sherds the majority do not appear to have ever been slipped or painted, though we cannot be positive of this. The painted sherds include eight that have a faded

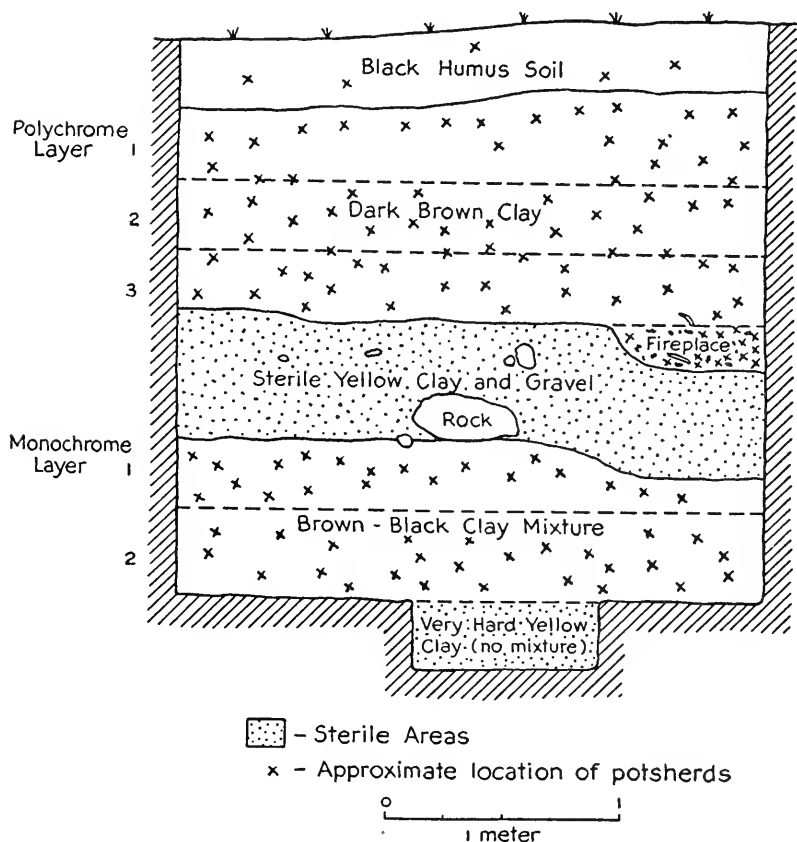


FIG. 32.—Cross-section of excavation A, near site 1, Los Naranjos, showing stratified cultural horizons.

red or pinkish slip (pl. 15, 1); two with a dull white slip or wash; and two that have definite areas painted a very dull red and black on the inner surface. Other decorative efforts are scant. A few sherds have raised ridges below the rim (pl. 15, *i*, 1), one has such a ridge with regular indentations, and a few sherds have simple, linear designs incised on the outer rim or body. If the present sample is at all adequate, this, the oldest known Lake Yojoa pottery, appears

to be the most primitive ceramic type yet encountered in Honduras. Technically, since a few sherds are painted, we should designate this ware as Yojoa bichrome. Actually, the great majority of sherds are unpainted and all of them are definitely inferior in both texture and finish to either the Playa de los Muertos Bichrome or the Santa Rita (farm 17) Bichrome wares. For this reason we have tentatively designated it as Yojoa "Monochrome", subject to change when the results of larger excavations yielding adequate ceramic samples are at hand.

Equally puzzling is the relationship of this Yojoa "Monochrome" to the two vessels excavated by Mr. Rittenhouse in this immediate vicinity. Both these vessels are well modeled, incised, and painted red and buff (pl. 15, *a*, *b*). Both originally had spouts. They are undoubtedly closely allied, if not identical, with the old Playa de los Muertos Bichrome (pls. 10, 11, and figs. 17, 18). Yet not one of our sherds from the deep stratum is positively of this type. We have no reason to doubt that the general location of the two Rittenhouse vessels was substantially as reported. It is apparent, therefore, that our Yojoa Monochrome is either a strangely isolated sample of crude, domestic ware, actually pertaining to the Playa de los Muertos Bichrome, or else that both Yojoa Polychrome, Playa de los Muertos Bichrome, and a new type, Yojoa Monochrome, all occur in shallow deposits on the northern borders of Los Naranjos.

Other artifacts from the older horizon at Los Naranjos included three figurine fragments (pl. 15, *e*, *j*). All are of solid, baked clay, and none are slipped. The crudely modeled little head (pl. 15, *e*) has a knot of hair on the back, and the body (pl. 15, *j*) has broad modeled and grooved buttocks which have been smoked black. Head and body are from different figurines. The third figurine torso is also of coarse, dull buff pottery. It is somewhat similar to the old Playa de los Muertos horizon figurine torsos (pl. 11, *t-v*), but is not so well modeled and has no breasts. Ground stone artifacts from this older Yojoa horizon include one small rectangular mano with ground sides and battered ends; one small rectangular stone (pl. 15, *n*) of unknown use; and a fragment of ground sandstone (pl. 15, *t*) which may be from a simple metate, although it has uneven grinding surfaces on the two sides. There are no true prismatic flake fragments from this horizon. There are, however, several irregular flakes of obsidian (pl. 15, *m*), and one irregular prismatic flake with a side point which also shows a use retouch. There is one rather large, gray flint side scraper and a flint flake. Here again, definite conclusions are precluded

by the small size of the present sample, but both the figurine and artifact fragments, like the pottery, show unique types.

There can be no doubt that, just below the elaborate polychrome horizon at Los Naranjos, there occurs another cultural level which appears to be surprisingly primitive. When it is remembered that our deepest excavations at Los Naranjos were slightly less than 3 meters, it can be seen that here is an area where deep excavations may yet furnish evidence regarding the truly simple cultures of Central America. On the Ulua, where we conducted our largest and deepest excavations, we were eventually stopped by reaching the water level. At Lake Yojoa this was not the case. A larger expedition, with adequate time and equipment, providing it is not led too far astray by the richer polychrome deposits, should be able to work out a most important sequence of human occupation in this immediate region.

OTHER SITES

Seeking for a deep Yojoa polychrome refuse heap suitable for stratigraphic analysis, we conducted a small excavation about 1 kilometer northeast of El Eden (see site 2, near that village, map, fig. 20). Miguel had brought us a number of polychrome sherds from this place, his sample including a dark brown and highly polished tripod bowl fragment with delicate geometric incisions on the body, an incensario fragment with rather elaborate geometric painted designs, and a small whistle shaped like a turtle. This sherd deposit was located in the abrupt face of a steep bank terminating a small, densely wooded arroyo. This arroyo led down toward one of the deep sink-holes which here mark the course of the Rio Blanco. The region is a maze of small, abrupt canyons or sink-holes, and is covered by unbelievably dense bush.

We dug a trench, 3.5 meters long and 1 meter wide, along the face of the bank, encountering our first potsherd at a depth of 40 centimeters. From this point down all artifacts were segregated according to horizontal levels averaging 30 centimeters in depth. Unfortunately, only three levels were encountered when we ran into sterile yellow clay. The exposed surface of the bank below this point appeared devoid of any human detritus. The upper 30-centimeter level contained a number of well-executed fragments of polychrome ware with highly conventionalized Mayoid designs. A tripod leg proved to belong to the dark brown and incised dish fragment secured earlier by Miguel. A number of heavier polychrome sherds had geometric designs in red and black, suggesting the Bold Geometric Ulua type,

but no definite Bold Animalistic sherds occurred. Crudely painted and occasionally incised sherds of domestic ware were fairly abundant in all levels. The middle layer yielded one conventionalized Mayoid sherd similar to the above, and a considerable number of red and black or orange sherds with designs suggesting the Bold Geometric. Definitive Bold Animalistic designs were lacking. The bottom level was similar but lacked both definitive Mayoid or Bold Animalistic designs, although several badly eroded polychrome sherds may have been of these types. To sum up, the El Eden polychrome site proved negative so far as any obvious stratification of ceramic types was concerned. The absence of definite Bold Animalistic type sherds is interesting but hardly significant, owing to the small sherd sample.

At excavation B, Los Naranjos (near site 1, map, fig. 20), a similar stratigraphic excavation was made. Here, again, only three 30-centimeter levels of polychrome sherds were obtained, the depth of the upper Yojoa Polychrome deposit being similar to excavation A (fig. 32). The top level contained rim fragments of small bowls, many of which had thickened lips. These sherds have conventional and rather massive red and black designs on orange and, in one case, white, backgrounds. Three basal fragments, one flat, one dimpled, and one annular, occurred. The latter is a dark brown, almost black, overfired piece. The middle level contained sherds with similar, conventionalized Mayoid designs, and a few with well-executed and isolated serpent motifs. A few sherds from this level are of the Bold Animalistic type. Basal fragments include two flat and two dimpled bottoms. The lowest sherd level included a bowl fragment with an elaborate open-winged bat (like pl. 3, *b*; Gordon, 1898). Several rim sherds from vertical-walled Mayoid vases have rows of typical Ulua conventionalized faces, and a fragment of a tripod plate has a similar design motif. In addition, there are a number of dull orange sherds with more conventionalized black and red geometric designs. From this lowest level comes a splendid Mayoid vase (pl. 12, *a*) encountered in a broken condition at a depth of 1.25 meters in the original excavation B test pit. This vase, with a definite rim, marked entasis, and a flat bottom, has an orange slip with complex anthropomorphic and glyph designs in brownish yellow, purplish red, and black. Thus, although the evidence is slender, there is some suggestion that the Lake Yojoa Polychrome wares exhibit the same trend from the more realistic to the conventional as was true of Ulua Polychrome pottery decoration. The occurrence at La Ceiba of both an extremely conventionalized Bold Animalistic vase (pl. 13, *a*) at a depth of only 15 centimeters, and a splendid, realistic Mayoid

vase (pl. 1) at a depth of 1.25 meters furthers this possibility. That both the more realistic and the more conventional aspects of the Mayoid and the Bold Animalistic tradition occur in the shallow Lake Yojoa Polychrome sites is certain. Their exact interrelationship, however, remains to be demonstrated.

Two other sites on the north end of Lake Yojoa may be briefly mentioned. The first of these is a little island, called merely, La Islita. It is near the shore between Jaral and Agua Azul (see map, fig. 1). Yde (1936, p. 30) describes a stone serpent head from this place which, subsequent to their visit, was reported to have been smashed by natives looking for treasure. He refers to, but does not reproduce, a photograph of this statue. Our guide brazenly showed us a simple cylindrical statue, apparently anthropomorphic and about 1 meter tall, the head and face of which had been completely smashed by him in a futile search for treasure! Only a carved ear remained and the rounded pediment which was like the simplest statue at Los Naranjos (pl. 16, 1). He did not know of the stone serpent head but claimed a similar anthropomorphic statue had been taken from the island to Tegucigalpa. Another man told us of a stone serpent head that had been found on this island, but said that local people had thrown it in the lake! The island is very steep and densely wooded. On top of one of the hills are a number of low, irregular mounds, some of which are covered with rock slabs. Our guide had dug pits in several of these and claimed to have found a few pieces of painted pottery. The soil of the mounds is a red clay. Aside from a few coarse brown sherds we saw no pottery at the site. There are said to be other mounds of a similar nature on the island, which we did not see. It is sincerely to be hoped that this interesting site may be scientifically worked by archeologists before it is completely ruined.

The other site is a group of three impressive mounds located in the open pine and savannah country about 2 kilometers northwest of the ranch house at Agua Azul (see map, fig. 1). The largest mound, to the north, is conical with a flattened top. It is approximately 7 meters high by 9 meters across, and is flanked to the west and south by a terrace edged with straight walls of large boulders about 1 meter in height. The west wall is about 5 meters from the edge of the mound and the south wall about 6 meters from it. The south wall is composed of several thicknesses of stone and terminates just east of the center of the mound. The west wall is only one stone thick and terminates just beyond the north edge of the mound. About 10 meters south of the edge of this terrace are two more parallel mounds. The mound to the east has an approximate length of 7 meters, and a

height of 5 meters. The mound to the west is smaller and steeper, being about 4 meters long and perhaps 3 meters high. Local men from Siguatepeque have excavated a small hole in the terrace south of the big mound and a large trench, 5 meters wide and nearly 6 meters deep, on the west side of the same mound. The earth wall of this trench shows successive curving layers of black charcoal, suggesting that the mound had been built up at different times and the remains of fires on the top had been scattered down the sides. The small pit on the terrace showed nothing. We were unable to find any potsherds, either in the cut or on the surface. According to local report the original diggers encountered nothing but a very little broken pottery. This is a striking mound group and, as already mentioned, seems similar in some ways to the "cut stone mound" which is buried in the dense bush near La Ceiba (site 3, map, fig. 20).

This concludes the list of sites visited by us around the north end of Lake Yojoa. We have since heard that local pot hunters have opened up a new series of ancient cemeteries between La Ceiba and Agua Azul. Other sites are reported in the mountains to the north (see map, fig. 20), at Saucé, and elsewhere around the lake, but we lacked time to visit these.

SUMMARY AND TENTATIVE CONCLUSIONS

The present reconnaissance of the Ulua-Yojoa region opens promising vistas. It reveals incomplete but considerable sequences of local development, and it demonstrates that the interplay of northern and southern cultural forces, so strongly suggested by linguistic, ethnographic, and historic sources, is very definitely reflected in the archeological record.

Since ceramic remains constitute the most abundant and helpful guides in attaining any understanding of the development of the prehistoric cultures of northwestern Honduras, we may preface our brief summary by a table showing the sequence and groupings of Ulua-Yojoa ceramic types as known at present (table 1). Of these the Naco Polychrome is definitely historic and represents, apparently, the late Nahuatl occupation of the region. Spinden, Tozzer, Mason, and Vaillant, who have examined this material, state that it appears to be related to certain late prehistoric wares of Mexico. Naco Polychrome pottery will probably be found at other sites occupied or influenced by these intrusive Nahuatl peoples. It may occur at Tenampua (compare Popenoe, 1936, p. 572 and fig. 2). In the same way that the occurrence of Spanish crockery in association with Naco Polychrome sherds connects the site with the historic period, so the occurrence of

simply decorated Ulua Polychrome sherds (pl. 3, *b*) in Naco refuse mounds indicates that other, local cultures were contemporaneous in the region. Little attention has as yet been paid to the historic and late prehistoric cultures of the Jicaque and other local inhabitants of northwestern Honduras.

TABLE 1.—*Apparent Sequence of Ceramic Types in Northwestern Honduras.*

	Ulua	Yojoa
Historic:	Naco Polychrome	
Prehistoric:	(surface mounds?)	
(late)	Ulua Polychrome (including)	Yojoa Polychrome (including)
↓	<div style="display: flex; align-items: center;"> <div style="margin-right: 20px;"> Mayoid { Upper Lower </div> <div> Bold Geometric { Upper Lower </div> </div>	<div style="display: flex; align-items: center;"> <div style="margin-right: 20px;">Mayoid</div> <div>Bold Animalistic</div> </div>
(to)		
	Ulua Bichrome (Santa Rita)	(here?)
	Playa de los Muertos Bichrome (P.d.l.M.)	Yojoa "Monochrome" (Los Naranjos)
↓		↑
(early)		(or here?)

TABLE 2.—*Probable Correlation between present Ulua Polychrome Classification (Table 1) and those of Gordon (1898) and Vaillant (1927)*

Ulua Polychrome	<div style="display: flex; align-items: center;"> <div style="margin-right: 10px;">{</div> <div>Upper Mayoid</div> </div> <div style="display: flex; align-items: center;"> <div style="margin-right: 10px;">{</div> <div>Upper Bold Geometric</div> </div>	Gordon's B	Vaillant's III and IV
		Gordon's C	Vaillant's V
Ulua Polychrome	<div style="display: flex; align-items: center;"> <div style="margin-right: 10px;">{</div> <div>Lower Mayoid</div> </div> <div style="display: flex; align-items: center;"> <div style="margin-right: 10px;">{</div> <div>Lower Bold Geometric</div> </div>	Gordon's A	Vaillant's I and II
		Gordon's C	Vaillant's V

The prehistoric polychrome wares of the Ulua have been classified on typological grounds by Gordon (1898), and by Vaillant (1927). In general their classifications seem to accord with our stratigraphic findings as above (table 2). Gordon clearly distinguished the Bold Geometric as Type C, and the Mayoid as Types A and B, but has nothing to say regarding sequence. Vaillant makes a mistake when he assumes, on stylistic grounds, that the Bold Geometric (Ulua Polychrome V) developed out of the Mayoid style and was therefore later. Strong makes the same mistake in regard to the related Bay Island

Polychrome I (Upper Mayoid, plus southern influences) and the identical Bay Island Polychrome II (Upper Bold Geometric) (1935, p. 145). Actually the Mayoid and the Bold Geometric have been shown to be parallel developments; thus Vaillant's Ulua Polychrome V is contemporaneous with his Ulua Polychrome I and II (his Ulua Polychrome IV contains both Upper Mayoid and Upper Bold Geometric constituents), and Strong's Bay Island Polychrome I is, in all probability, contemporaneous with his Bay Island Polychrome II. Vaillant (1927, p. 266) was careful to point out the entirely tentative nature of his assumed sequences. Further, in regard to the Ulua Polychrome V (and Salvador Polychrome VI) he states: "There is a strong suspicion of the same non-Maya factors influencing both these styles. The source of the influence is not discoverable in Maya districts, and one thinks vaguely of the south and east, of Nicaragua, eastern Honduras, and Costa Rica to locate a source" (1927, p. 170).

Recently Tschopik (1937), in a brief but valuable analysis of textile motifs on Gordon's Ulua Polychrome pottery, has independently pointed out this stylistic dichotomy. He groups Vaillant's Ulua Polychrome I-IV as Ware A [Mayoid], and the latter's Ulua Polychrome V as Ware B [Bold Geometric]. Tschopik points out that there are consistent differences in both form and decoration between the two, and that A is Mayoid, whereas B has a definite relationship in form and decoration with ceramic types from Salvador, Nicaragua, and Costa Rica. He, too, repeats the theory that naturalistic designs are apt to be earlier than geometric, suggesting that Ware A is earlier than Ware B, thus falling into the same error as Vaillant and Strong.

At Santa Rita these two major styles (Mayoid and Bold Geometric) are intermixed throughout almost 4 meters of Ulua Polychrome deposits. Although they blend in certain intermediate types of vessels, each style in general keeps to its own particular genius, and each shows a parallel development from a finer and somewhat more realistic decoration in the lower levels, to a more conventionalized and geometric decoration in the upper levels. Thus, the Lower Mayoid has priestly, processional, and "dancing" figures in open panels, whereas the Upper Mayoid has florid, conventionalized, over-all designs, geometric motifs and, often, animal head lugs. The Lower Bold Geometric has intricate linear and geometric designs with remarkable, cursive animals or birds in open panels, whereas the Upper Bold Geometric becomes simpler, drops the animals, but retains textile and geometric designs. At Las Flores, also, both the Mayoid and the Bold Geometric styles occur in the same excavation, but here both are of the upper and later, conventionalized type. It is worth noting that the only

metal object recovered in any of our excavations, a small copper fish-hook, came from these levels at Las Flores. The Ulua Polychrome horizon overlying the deep stratum at Playa de los Muertos is also late. Here only the Upper Mayoid and Upper Bold Geometric occur. It is undoubtedly significant that the typical, swollen, monkey-handled olla form of the Bold Geometric tradition (pl. 7, *a-d*), and the vertical-walled vase form of the Mayoid tradition (pl. 8, *a-b*), both persist practically unchanged throughout the entire Ulua Polychrome series. This occurrence argues rather strongly against any very considerable time period being assigned to the Ulua Polychrome period.

The polychrome wares of Lake Yojoa are closely related to those of the Ulua. Not only does Yojoa Polychrome ware contain a large number of forms and motifs identical with those of the Ulua Polychrome, but it also manifests a very similar division into two major stylistic traditions. In general, however, Ulua and Yojoa Polychrome ware vessels are distinguishable. The Yojoa Mayoid type, as well as the Bold Animalistic type, finds many close parallels in polychrome vessels from eastern Salvador (see Vaillant, 1927, figs. 35-40). It seems strange that no Plumbate ware whatsoever was recovered in any of our excavations, either on the Ulua or at Lake Yojoa. The Bold Animalistic type from Lake Yojoa differs from the Ulua Bold Geometric in the relative rarity of monkey-handled ollas and the prevalence of bird, monkey, alligator, and other animal design motifs. Regarding the internal development of Yojoa Polychrome ware decoration, there is some very slight evidence that it parallels the trend of the Ulua Polychrome series from better executed realistic, to conventional and geometric design. However, the 1½ meters of Yojoa Polychrome deposits so far investigated have not as yet yielded very satisfactory evidence in this regard. The fact that Ulua Polychrome deposits occur throughout 3 to 4 meters of alluvial and cultural deposition, whereas the known Yojoa Polychrome refuse deposits are less than 2 meters in depth, is undoubtedly significant. In our opinion, however, this discrepancy is probably due to the very different physiographic conditions in the two regions, rather than to differences in time.

Of the three wares that have been stratigraphically established as earlier than the Ulua-Yojoa Polychrome series, the Playa de los Muertos Bichrome (table 1, and pls. 10, 11) is the most clearly defined. This is the type D of Gordon (1898). Vaillant (1934) has pointed out that this horizon contains a majority of traits, mainly ceramic, that are characteristic of the Q complex. It is undoubtedly significant that, whereas Playa de los Muertos Bichrome ceramics

represent an advanced pottery type so far as texture, surface finish, modeling, and incising are concerned, they appear to mark an experimental and inept stage in the use of surface painting. Especially characteristic of this horizon are highly polished, modeled and spouted forms; flat-bottomed, vertical-walled vases; low dishes with flaring incised walls or everted, flat, incised lips or both; and solid female figurines, which may or may not have a white slip. There is considerable resemblance between the simple but effective modeling of these figurines (pl. 11, *t*, *u*, *v*) and the stone statue of a man or ape at Los Naranjos, Lake Yojoa (pl. 16, fig. 3). These traits, plus the occurrence of jadeite artifacts and the varied experiments with painted decoration, all indicate that here was an early and potent cultural manifestation of more than local significance. In so far as data are available (R. E. Smith, 1936, and Uaxactun sample sherd collections), we see considerable resemblance between this Playa de los Muertos Bichrome ware and the two earliest stratigraphic periods at the old Maya city of Uaxactun. These have been termed Mamon and Chicanel, and both precede the Maya Polychrome period.

The determination of the northern and the southern extent of the Playa de los Muertos horizon is one of the important problems in Middle American archeology. Even more important is the determination of the simpler ceramic horizons from which it developed. In Honduras we have as yet no clues to this earlier period unless the so-called Yojoa "Monochrome" (pl. 15, *c-w*) is as truly primitive as it superficially appears, and can be demonstrated as stratigraphically earlier than the developed Playa de los Muertos culture. The later break, between the Playa de los Muertos Bichrome and the Ulua Polychrome, is in part bridged by the deepest cultural horizon at Santa Rita containing Ulua Bichrome ware. The most outstanding feature of the Ulua Bichrome ceramics is the presence of Usulatan ware sherds. According to Lothrop this is "the earliest painted pottery now known from Central America", and, although it occurs occasionally in the form of trade pieces at Old Empire Maya sites, it seems to center in Lenca territory in eastern Salvador (1933, pp. 47-51). There is rather close resemblance between our Usulatan sherds with short, solid legs (pl. 9) and the early Chukumuk pottery from Lake Atitlan in the highlands of Guatemala (Lothrop, 1933, p. 49). Similarly, the tetrapod Usulatan bowl recovered by Gordon at a depth of "26 feet" in his Playa de los Muertos excavations is of an identical type. Thus, there is a linkage in this regard between the deep horizons at Playa de los Muertos and at Santa Rita, despite the fact that our own sample of Playa de los Muertos Bichrome ceramics

contains no definite Usulután ware. In addition, this clear linkage between early Ulúa and early Guatemalan highland cultural horizons is of great interest. We have assumed that Ulúa Bichrome is somewhat later than the Playa de los Muertos Bichrome on stylistic grounds and because the sterile area separating the former from the Ulúa Polychrome is thin compared to that separating the Playa de los Muertos Bichrome from the overlying Ulúa Polychrome (compare fig. 6, and fig. 16). This, however, is at best a dubious procedure, since we do not as yet know the physiographic nature of either sterile stratum. Moreover, it must be remembered that only the Upper Mayoid and Bold Geometric Ulúa Polychrome types occur in the overlying cultural stratum at Playa de los Muertos, whereas both these and the earlier Lower Ulúa Polychrome wares occur above the Ulúa Bichrome at Santa Rita. These details, like the cultural and temporal placing of the puzzling Yojoa "Monochrome" ceramics and the "Chorotegan" stone statues at Los Naranjos, must await further excavation.

Tracing the relationship of the native cultures of northwestern Honduras backward from the known historic, we have already verified the presence of a late Nahuatl migration from Mexico through the finds made at Naco. Similarly, in the Ulúa Polychrome period we find two interlocked but distinct styles occurring in the same sites, the Mayoid and the Bold Geometric, which at Santa Rita persist and develop simultaneously over a considerable period. Lake Yojoa Polychrome is also composed of a Mayoid and a so-called Bold Animalistic tradition. This original fission and subsequent parallelism of both Ulúa and Yojoa Polychrome ceramic development has obvious sociological as well as archeological implications. At both Ulúa River and Lake Yojoa Polychrome sites one of these styles is Mayoid and the other is of southern origin. For linguistic and ethnographic reasons previously discussed, it seems highly probable that the Bold Geometric element of the Ulúa Polychrome was contributed by Jicaque peoples, whereas the very similar Bold Animalistic element in Yojoa Polychrome was due to the related Lenca. Since the Mayoid element comprises about one half of the Ulúa and Yojoa Polychrome ceramic remains, it can hardly be explained as due solely to trade or indirect influence. It seems far more logical to assume that intermixed Maya, Jicaque, and Lenca peoples were living together at these sites and that perhaps the pottery-makers of each ethnic group clung to their own art styles over a considerable period. The quite remarkable florescence and the high and complex artistic attainments of the Ulúa

and the Yojoa Polychrome periods are in all probability the direct results of this cultural and physical amalgamation.

We have at present no means for dating the exact period represented by these Lenca and Jicaque styles which apparently stem from Nicaraguan and Nicoyan culture centers to the south. On the other hand, there is in the nearby Maya city of Copan a series of dated monuments ranging from 9:11.0.0.0 (stela 3) to 9:17.12.0.0. (stela C) (or, roughly, according to the Goodman-Thompson-Martinez correlation, between 650 and 800 A. D.), in association with which there occur pottery vessels (Vaillant, 1927, and Lothrop, 1933, p. 66 and 1936 b, p. 69). We have attempted to correlate our Ulua and Lake Yojoa Polychrome series with Vaillant's classification of Copan wares, but owing to the selective nature of the Copan collections, as well as the paucity of illustrative material, this has proved impracticable for the present. The Copan ceramic series in the Peabody Museum, as a whole, seems quite distinct from the Ulua-Yojoa Polychrome wares, although numerous similarities do exist. Vaillant points out the occurrence of Ulua Polychrome sherds at mound 36 in Copan, a point we were able to verify for ourselves at the site, but there is reason to believe that these deposits are later than the Copan series or perhaps intrusive. According to Vaillant (1927, p. 271) the trend of the Ulua Polychrome wares "suggests the years after the fall of Copan." If this is the case, it may serve to point out when the Maya Old Empire dispersal into Salvador and northwestern Honduras took place and how their developed polychrome wares came to be grafted on to those of the Lenca, Jicaque, and, probably, the Pipil, with whom the various Maya groups settled. When adequate stratigraphic studies of the entire range of Copan ceramics have been made and correlated with the ceremonial series from the stelae vaults, described by Vaillant, there is reason to believe that the Ulua-Yojoa Polychrome series may also be approximately dated.

Such excavations should also throw light on the origin or derivation of the southern Mayoid Polychrome ceramic tradition. Did it arise from a groundwork similar to the Playa de los Muertos culture in the Peten, perhaps at Uaxactun or Holmul, spread from there to Copan, and thence to Salvador and the Ulua? Or are there intermediate stages between the developed Polychrome and the Playa de los Muertos horizons present but as yet unknown in Honduras, at Copan, or in Salvador? An even more basic problem concerns the suggested relationship between the ceramics in the oldest horizons at Uaxactun in the Peten and Chukumuk in the Guatemalan highlands, with the Playa de los Muertos Bichrome and Ulua Bichrome

wares respectively. Lothrop (1933, p. 62) believes that the elements shared in common by the earliest known cultural horizons in the highlands and the Atlantic lowlands of Guatemala were derived, not from one another, but from a parent culture to the south. When the Uaxactun materials are available, the rôle of the southern Playa de los Muertos culture as a donor or a recipient may be tested. These are questions for the future but, thanks to the growing scientific vogue of the shovel, they are questions that may soon be answered.

LITERATURE CITED

BANCROFT, H. H.

1882. The native races of the Pacific States, vols. 1-5. San Francisco.

1883-7. History of Central America, vols. 1-3. (Vols. 6, 7, and 8 of Bancroft's Works. San Francisco, 1882-1890.)

BLACKESTON, R. H.

1910. Recent discoveries in Honduras. *Amer. Anthropol.*, n. s., vol. 12, no. 4, pp. 536-541.

BLOM, FRANS, GROSJEAN, S. S., and CUMMINS, HAROLD

1933. A Maya skull from the Uloa Valley, Republic of Honduras. *Tulane Univ. Studies in Middle America*, Publ. 5, no. 1. New Orleans.

COLECCIÓN DE DOCUMENTOS INÉDITOS relativos al descubrimiento, conquista y colonización de las posesiones Españolas en America y Oceania, tomos 1-41. Madrid, 1854-84.

CUMMINS, HAROLD. See BLOM, FRANS, GROSJEAN, and CUMMINS.

DIAZ DEL CASTILLO, BERNAL

1908-16. The true history of the conquest of New Spain, vols. 1-5. Edited and published in Mexico by Genaro Garcia. Translated by A. P. Maudsley. Hakluyt Soc. Publ., ser. 2, vols. 23-25, 30, and 40. London.

GORDON, GEORGE BYRON

1898. Researches in the Uloa Valley, Honduras. *Mem. Peabody Mus. Archaeol. Ethn.*, Harvard Univ., vol. 1, no. 4. Cambridge.

GROSJEAN, S. S. See BLOM, FRANS, GROSJEAN, and CUMMINS.

HABEL, S.

1880. The sculptures of Santa Lucia Cosumalwhuapa in Guatemala. *Smithsonian Contr. Knowl.*, vol. 22, art. 3, pp. 1-90. Washington.

DE LAS CASAS, BARTHELEMI

1922. *Œuvres de Don Barthélemy de Las Casas, évêque de Chiapa*. Edited by J. A. Llorente. Vols. 1-2. Paris.

LEHMANN, WALTER

1910. Ergebnisse einer Forschungsreise in Mittelamerika und Mexico, 1907-1909. *Zeitschr. Ethnol.*, vol. 42, pp. 687-749. Berlin.

1920. *Zentral Amerika*. Vols. 1-2. Berlin.

LOTHROP, S. K.

1921. The stone statues of Nicaragua. *Amer. Anthropol.*, n. s., vol. 23, no. 3, pp. 311-319.

1933. Atitlan. An archaeological study of ancient remains on the borders of Lake Atitlan, Guatemala. *Carnegie Inst. of Washington. Publ.* 444.

- 1936 a. Sculptured pottery of the Maya and Pipil. *Maya Research* (Mexico and Central America), vol. 3, no. 2, pp. 140-152. New Orleans.
- 1936 b. Zacualpa. A study of ancient Quiche artifacts. *Carnegie Inst. of Washington*, Publ. 472.
- MASON, OTIS T.
- 1889 a. How to straighten a spear shaft. *Amer. Anthropol.*, ser. 1, vol. 2, no. 2, p. 158.
- 1889 b. Music in Honduras. *Amer. Anthropol.*, ser. 1, vol. 2, no. 2, p. 158.
- DE PALACIO, DIEGO GARCIA
1860. Carta dirijida al Rey de Espana. Año. 1576. (Original Spanish with English translation.) Squier's "Collection of rare and original documents and relations", no. 1. New York.
- POPENOE, DOROTHY H.
1934. Some excavations at Playa de los Muertos, Ulua River, Honduras. *Maya Research*, vol. 1, no. 2, pp. 61-86. New York.
1936. The ruins of Tenampua, Honduras. *Ann. Rep. Smithsonian Inst.* 1935, pp. 559-572.
- SPINDEN, HERBERT J.
1925. The Chorotegan culture area. *Compt. Rend. 21st Congr. Internat. Amer.*, Göteborg, 1924, pp. 529-545. Goteborg.
- SQUIER, EPHRAIM GEORGE
1858. The States of Central America. New York.
1859. A visit to the Guajiquero Indians. *Harper's New Month. Mag.*, vol. 19, no. 113, pp. 603-619. New York.
1860. Some account of the Lake of Yojoa or Taulebé, in Honduras, Central America. *Journ. Roy. Geogr. Soc.*, vol. 13, pp. 58-63. London.
1869. Tongues from tombs, or the stories that graves tell. *Frank Leslie's Illustr. Newsp.* New York.
1870. Honduras. Descriptive, historical, and statistical. London.
- SMITH, H. E.
1936. Preliminary shape analysis of the Uaxactun pottery. (Typed script, with illustrations reproduced photographically.) Guatemala.
- STONE, DORIS ZEMURRAY
1934. A new southernmost Maya City. *Maya Research*, vol. 1, no. 2, pp. 125-132. New York.
- STRONG, WILLIAM DUNCAN
- 1934 a. Hunting ancient ruins in northeastern Honduras. *Explorations and Field-Work of the Smithsonian Inst.*, 1933, pp. 44-48.
- 1934 b. An archeological cruise among the Bay Islands of Honduras. *Ibid.*, pp. 49-50.
1935. Archeological investigations in the Bay Islands, Spanish Honduras. *Smithsonian Misc. Coll.*, vol. 92, no. 14, pp. 1-176.
1937. Archeological explorations in northwestern Honduras. *Explorations and Field-Work of the Smithsonian Inst.*, 1936, pp. 75-82.
- THOMAS, CYRUS, and SWANTON, JOHN R.
1911. Indian languages of Mexico and Central America and their geographical distribution. *Bur. Amer. Ethnol. Bull.* 44.
- DE TORQUEMADA, JUAN
1723. Los veinte i un libros rituales i Monarchia Indiana, con el origen y guerras, de los Indios Occidentales. Madrid.

TOZZER, ALFRED M.

1930. Maya and Toltec figures at Chichen Itza. Proc. 23d Internat. Congr. Amer., New York, 1928, pp. 155-164. New York.

TSCHOPIK, HARRY, JR.

1937. Textile motifs from Uloa Valley pottery. MS., Peabody Mus., Harvard Univ.

VAILLANT, G. C.

1927. The chronological significance of Maya ceramics. Manuscript thesis submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, Harvard Univ.
1934. The archaeological setting of the Playa de los Muertos culture. Maya Research, vol. 1, no. 2, pp. 87-100. New York.

WELLS, WM. V.

1857. Explorations and adventures in Honduras. New York.

YDE, JENS

1935. Foreløbig Beretning on Nationalmuseets og Tulane Universitetets Ekspedition til Mellemamerika 1935. Særtryk Geogr. Tidsskr., vol. 38, nos. 3-4, pp. 137-155.
1936. A preliminary report of the Tulane University-Danish National Museum expedition to Central America. Maya Research (Mexico and Central America), vol. 3, no. 1, pp. 25-37. New Orleans.

EXPLANATION OF PLATES

PLATE 1

Processional figures on a Yojoa Polychrome vase, Mayoid type. Site 2, La Ceiba (13.2 cm high).

PLATE 2

Various Chamelecon and Uluá River sites

FIG. 1. Fragment of ball court ring *in situ*, Naco.

FIG. 2. Thin plaster walls, heart of mound 3, Naco.

FIG. 3. Excavation 1 and start of excavation 2 (right) at Santa Rita (farm 17).

FIG. 4. Site at Tres Piedras, showing mounds and plaza cross-sectioned by Chamelecon River.

PLATE 3

Naco sherds

a, c-w, Naco Polychrome; *b*, Uluá Polychrome sherds found at Naco.

PLATE 4

Naco sherds and artifacts

a, incensario; *b-g*, figurine fragments; *h*, whistle; *i, j*, spindle whorls; *k*, obsidian flake knives; *l*, clay bobbins; *m*, Spanish colonial crockery; *n-p*, textile-marked sherds; *q, s, t, u, v, x, y, z*, sherds with molded or carved designs; *r*, incised sherd; *w*, "candelarios."

PLATE 5

Upper Ulua Polychrome pottery types, Las Flores

a-e, Las Flores painted and incised vase sherds; *f-m*, Upper Mayoid type sherds; *n*, sculptured or molded Mayoid sherd.

PLATE 6

Upper Ulua Polychrome pottery types, Las Flores

a, human effigy (16.5 cm); *b*, vessel with "vestigial" spout (14 cm); *c*, Upper Mayoid jar (7 cm); *d*, sculptured or molded Mayoid jar (6.5 cm); *e* (5 cm), *f* (6.5 cm), jars of imitation Ulua marble bowl type.

PLATE 7

Ulua Polychrome, Bold Geometric pottery types, Santa Rita

a, Bold Geometric olla (12 cm); *b* (22 cm); *c* (30 cm); *d* Lower Bold Geometric olla type (30 cm); *e*, Bold Geometric tripod dish (7.5 cm); *f*, Bold Geometric tripod dish (10 cm). (*a-e*, Santa Rita; *f*, Naranjo Chino.)

PLATE 8

Ulua Polychrome, Mayoid pottery types, Santa Rita

a, Lower Mayoid type vase (20 cm); *b*, Lower Mayoid type vase (20 cm); deer effigy pot cover (19.5 cm); *c*, Mayoid type vase (17.8 cm); *e*, *f*, tripod plate, type uncertain (14.5 cm).

PLATE 9

Ulua Bichrome sherds, deepest level, Santa Rita

a-j, various sherds; *k*, obsidian scraper; *l*, pottery stamp; *m*, obsidian flake knife fragment; *o-s*, *u-z*, *aa*, *bb*, Usulután ware sherds; *t*, Lower Mayoid type sherds from just above sterile sand layer; *cc*, red-on-white sherd.

PLATE 10

Playa de los Muertos Bichrome sherds

a-h, polished orange-red to brown; *i-n*, polished dark gray to black; *o-s*, polished slate-gray to buff. (Lower cultural horizon, Playa de los Muertos.)

PLATE 11

Playa de los Muertos sherds and figurines

a-e, sherds with chalky white wash; *f*, *g*, *k*, red and black; *i*, *j*, *o*, red on buff; *h*, unslipped brown and red; *l*, *m*, red on white; *n*, gray on dull red; *p*, polished brown face; *q*, *r*, *s*, polished figurines with white slip; *t*, *u*, *v*, solid brown figurines (lower cultural horizon, Playa de los Muertos).

PLATE 12

Yojoa Polychrome vessels, Mayoid types

a, excavation B, Los Naranjos (25 cm); *b*, Aguacate (16.3 cm); *c* (10.7 cm); *d* (10.5 cm), Aguatal; *e*, Aguacate (9.5 cm); *f*, La Ceiba (12 cm).

PLATE 13

Yojoa Polychrome vessels

Bold Animalistic type: *a*, La Ceiba (15 cm); *b*, site 1, Los Naranjos (12.5 cm); *c*, Aguatal (10 cm); *d*, La Ceiba (11 cm); *e*, Effigy (type ?, compare fig. 7, *p*, p. 52), La Ceiba (11 cm); *f*, Mayoid type, Aguatal (11.5 cm).

PLATE 14

Yojoa Polychrome vessels

a (10.7 cm); *b* (10.2 cm), Bold Animalistic type, Aguacate; *c* (8 cm); *d* (10 cm), Bold Geometric or Bold Animalistic types, Aguacate and Los Naranjos, site 1; *e*, imitation Ulua marble bowl type, Aguacate (6.7 cm); *f*, carved brown ware, Aguacate (7.3 cm); *g*, bowl with negative painting, Los Naranjos, site 1, (6 cm); *h*, bird-shaped pot, Aguatal (7 cm).

PLATE 15

Early ceramic types at Lake Yojoa

a (11 cm); *b* (12 cm), Playa de los Muertos Bichrome type (?), Los Naranjos (exact provenience uncertain); *c*, *d*, *f-i*, *k*, *l*, *o-s*, *u-v*, Yojoa "Monochrome" sherds; *e*, *j*, figurine fragments; *m*, obsidian flake; *n*, *t*, ground stone artifacts. (*c-v*, lower cultural horizon at Los Naranjos, site 1, and excavations A and B.)

PLATE 16

Los Naranjos, Lake Yojoa

FIG. 1. Crude anthropomorphic statue.

FIG. 2. Stone serpent head.

FIG. 3. Stone torso and head.

FIG. 4. Mound 1, from the north near site 1.

FIG. 5. Section of trench at site 1, showing house floor and burial.



VARIOUS CHAMELECON AND ULUA RIVER SITES

- 1, Ball court at Naco; 2, mound structure at Naco; 3, excavation at Santa Rita (farm 17); 4, Tres Piedras site.



NACO SHERDS

b. Uluu Polychrome sherds at Naco.



NACO SHERDS AND ARTIFACTS
m, Spanish colonial sherd at Naco.



UPPER ULUA POLYCHROME POTTERY TYPES, LAS FLORES



UPPER ULUA POLYCHROME POTTERY TYPES, LAS FLORES



a



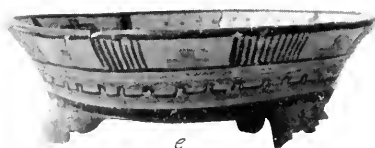
b



c



d

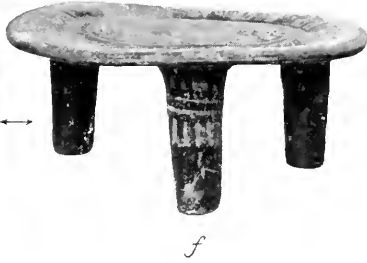
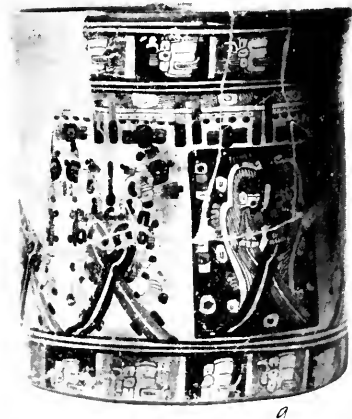


e

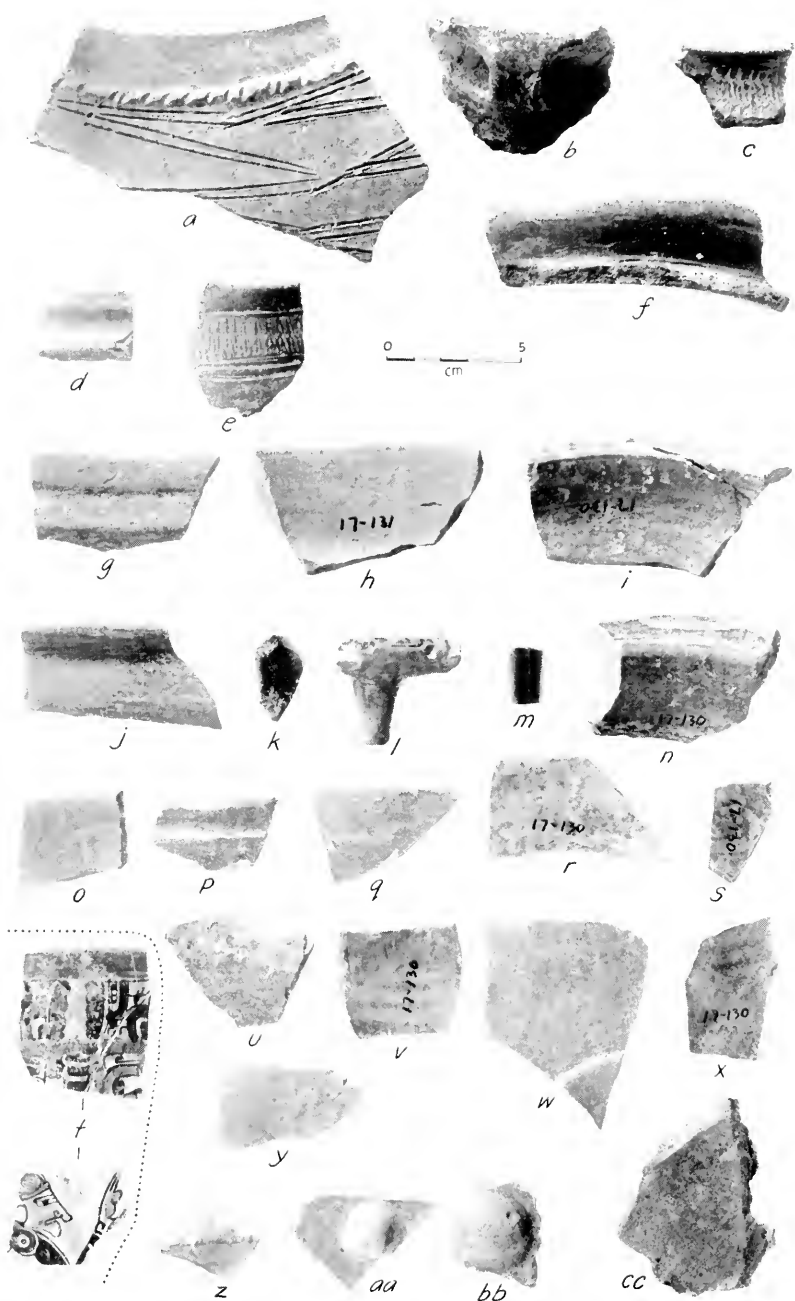


f

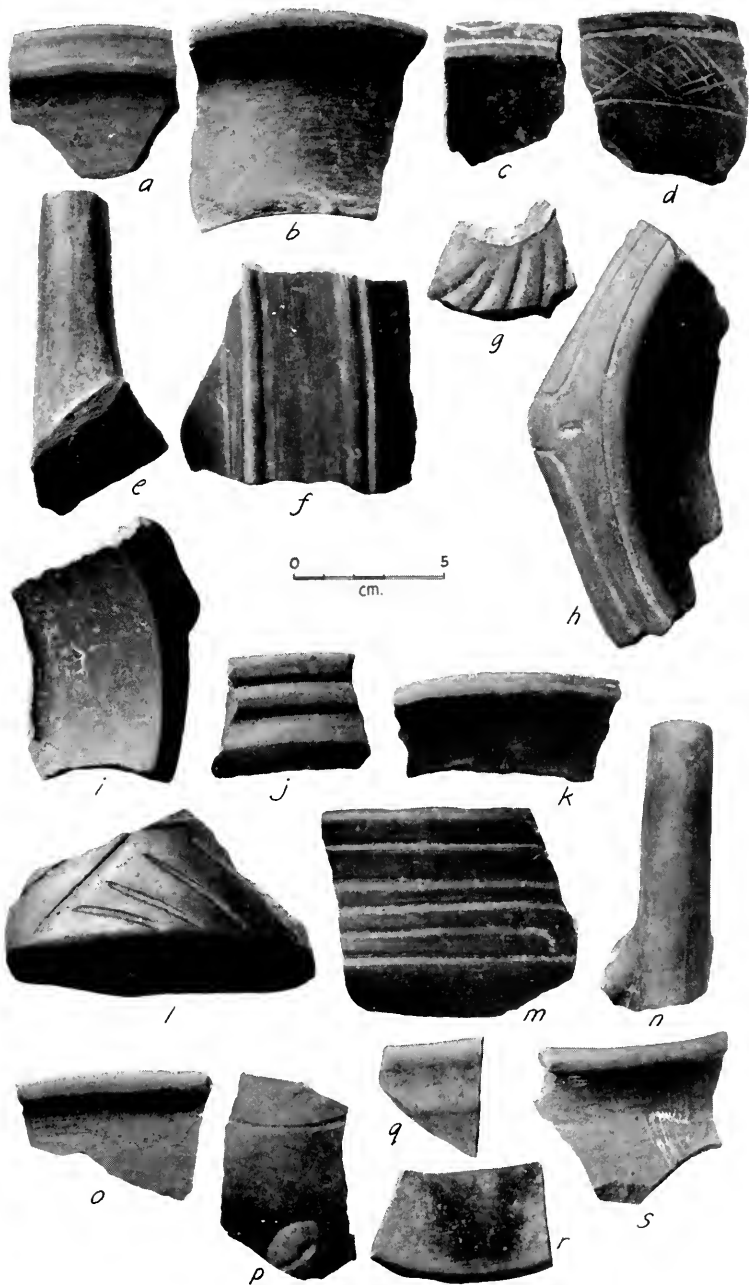
ULUA POLYCHROME. BOLD GEOMETRIC POTTERY TYPES. SANTA RITA
f, Naranjo Chino.



ULUA POLYCHROME. MAYOID POTTERY TYPES. SANTA RITA



ULUA BICHROME SHERDS, DEEPEST LEVEL, SANTA RITA
t, Lower Mayoid sherds on sterile sand layer above Ulua Bichrome horizon.



PLAYA DE LOS MUERTOS BICHROME SHERDS



PLAYA DE LOS MUERTOS BICHROME SHERDS AND FIGURINES



YOJOA POLYCHROME VESSELS. MAYOID TYPES



YOJOA POLYCHROME VESSELS. BOLD ANIMALISTIC TYPES
c, uncertain type; *f*, Mayoid type.



YOJOA POLYCHROME VESSELS, VARIOUS TYPES

a-d, Bold Animalistic and Bold Geometric; *e*, imitation Ulua marble bowl.



EARLY CERAMIC TYPES AT LAKE YOJOA

a, b, Playa de los Muertos Bichrome (?); *c-w*, Yojoa "Monochrome."



LOS NARANJOS, LAKE YOJOA

1, crude human statue; 2, stone serpent head; 3, stone torso and head;
4, mound 1; 5, section of trench, site 1.





SMITHSONIAN MISCELLANEOUS COLLECTIONS
VOLUME 97. NUMBER 2

PLANT GROWTH IN RELATION TO WAVE-LENGTH BALANCE

(WITH FOUR PLATES)

BY

EARL S. JOHNSTON

Assistant Director, Division of Radiation and Organisms
Smithsonian Institution



(PUBLICATION 3446)

CITY OF WASHINGTON
PUBLISHED BY THE SMITHSONIAN INSTITUTION
JANUARY 12, 1938

SMITHSONIAN MISCELLANEOUS COLLECTIONS
VOLUME 97, NUMBER 2

PLANT GROWTH IN RELATION TO WAVE-LENGTH BALANCE

(WITH FOUR PLATES)

BY

EARL S. JOHNSTON

Assistant Director, Division of Radiation and Organisms
Smithsonian Institution



(PUBLICATION 3446)

CITY OF WASHINGTON
PUBLISHED BY THE SMITHSONIAN INSTITUTION
JANUARY 12, 1938

The Lord Baltimore Press
BALTIMORE, MD., U. S. A.

PLANT GROWTH IN RELATION TO WAVE-LENGTH BALANCE

BY EARL S. JOHNSTON

Assistant Director, Division of Radiation and Organisms, Smithsonian Institution

(WITH FOUR PLATES)

INTRODUCTION

There can be little doubt that wave-length distribution exerts an enormous influence on the growth of plants. Numerous experiments show that stem elongation is greatly retarded under blue light, whereas an acceleration takes place in the red and near infrared regions. Chlorophyll production takes place better toward the red than toward the blue end of the visible spectrum. Phototropic sensitivity is greatest in the blue and zero in the red. For equal amounts of energy falling on the leaf, two maximal regions of CO₂ absorption have been found—one in the red, the other in the blue. It thus appears that a wave-length region best suited to a given plant process may be entirely without effect upon another.

In plant nutrition studies, experiments have shown that there is a general balance in the proportionate amounts of mineral elements of a nutrient solution that brings about a favorable growth response in plants. Although there may be considerable latitude in the ratio of amounts of elements in such a solution, it may be said that a balanced condition exists.

In a somewhat analogous manner, it is possible to think of the light requirements of plants as a balanced condition of intensities of different wave lengths which bring about good plant growth. Both light intensity and wave-length distribution vary to a considerable extent over the earth's surface. Likewise the character of the vegetation varies. Since plants have been growing on the earth for countless ages, it is reasonable to assume that their physiology is adjusted best to sunlight. Although there is experimental evidence to show that different processes go on better in some wave-length regions of the spectrum than in others, yet the best growth, when all the processes are considered simultaneously, apparently takes place in the natural

light of the sun. A direct experimental comparison between sunlight and artificial light is, of course, difficult to make because of the great number of variables entering into the problem.

Numerous experiments have been made for the purpose of growing plants under artificial illumination. The object of many such experiments was to find a satisfactory artificial light which could be operated economically on a commercial scale. In other experiments the technical and scientific aspects were the main objectives. So far as is known, there is no available light source which is like that of the sun in its wave-length distribution. Plants have been grown fairly successfully in a few instances under well-controlled laboratory conditions, but the problem is by no means solved. It may even be found that plants can be grown normally under greatly reduced intensities of light provided a proper proportion between the intensities of its component wave lengths is worked out.

The purpose of the present report is to discuss briefly some preliminary experiments dealing with the question of a wave-length balance of artificial light.

EXPERIMENTATION

In the experiments herein described, plants were grown between two different light sources. Three or more types of lights could be used, but for this preliminary survey it was thought best to limit the wave-length distribution to two types. All the experiments were conducted in a small room (approximately 15 x 10 ft. x 8 ft. high) the walls and ceilings of which were painted a flat black to minimize scattered light effects. Both temperature and humidity were automatically controlled. The plants were grown in 1-quart jars containing nutrient solution. Each culture was placed on a small rotating table and usually grown for 3 weeks with a daily light period of 12 to 18 hours. By constantly rotating the plants (3.4 r.p.m.) on an axis parallel to their stems, the phototropism of these stems was reduced to zero. The leaves in some experiments showed phototropic response. The wave-length distribution depended upon the light source. The intensity was regulated largely by the distance the culture was placed from the light.

In an earlier paper Johnston (1932) found that the excess of near infrared of the Mazda lamp caused a distinct yellowing of tomato leaves. If this region of the spectrum was not actually destructive to chlorophyll, it was of little or no benefit to its formation. It would thus appear that more nearly normal color could be obtained by re-

ducing the infrared or by increasing the intensity of the rest of the spectrum. An experiment was therefore planned in which this was partially accomplished by building up the blue end of the spectrum.

Experiment 1.—Two 1,000-watt projection Mazda lamps (115 v.) were placed 1 meter apart. Surrounding each lamp was a clear Pyrex thermos bottle blank fitted with a water inlet and outlet. The radiation of each lamp was thus filtered through 5 mm of water. The constant flow of water through this jacket was a great aid in maintaining a constant temperature condition in the room, since a great deal of heat was thus removed.

A copper sulphate (sp. gr. 1.08, about 8 percent) filter (6 cm thick) was placed in front of one of the lamps. This was the added blue light source. The individual rotating plant cultures were located at positions relative to these two light sources which gave the intensity values expressed as watts/cm² in table 1.

TABLE 1.—*Radiation intensities and plant data from experiment 1*

Culture no.	Light intensity watts/cm ²			Stem ht. cm	Total dry wt. gram
	White	Blue	Total		
1.....	.0396	.0006	.0402	5.0	.086
2.....	.0285	.0010	.0295	7.1	.102
3.....	.0166	.0014	.0180	6.1	.043
4.....	.0064	.0027	.0091	6.3	.025
5.....	.0046	.0054	.0100	3.8	.019

Marglobe tomato seeds were sprouted between moist filter paper at a temperature of 25° C. for 3 days. The sprouted seeds were then transferred to a germination net, and after about a week of growth five similar seedlings were selected and set out in quart jars, one per jar, and placed on the five small rotating tables. After 2 weeks of growth these plants were measured and dried in an oven at 103° C. to obtain the dry weight. These data are also shown in table 1.

Because of the meagerness of data, no definite conclusions can be drawn. The first three plants were heavier than similar ones grown in the north and south laboratory windows. Although the total intensity of no. 1 was greatest, yet maximum dry weight occurred in plant no. 2. Here the added blue radiation was about 3 percent of the total as compared to 1.5 percent in plant no. 1, which was yellow-green in color. Plant no. 2 was a light green when compared to plants 3, 4, and 5, whose percentage of added blue to total radiation were respectively 8, 30, and 54.

Experiment 2.—The next experiment was very similar to that just described. Here again individual variation was too great to draw any accurate conclusions.

Experiment 3.—In the next experiment three duplicate sets of tomato plants were grown under three different sets of light conditions. In front of one lamp a Corning heat-absorbing 212 percent red filter was placed. In front of the other lamp a filter jar containing a M/2 CuSO_4 solution was placed. Both filters cut off at 6040 Å, the CuSO_4 solution transmitting light of shorter wave length and the Corning filter transmitting light of longer wave length. Two duplicate sets of cultures were placed between these filtered light sources. A third set was located to the rear of the blue filter light in such a position that the plants received only the full Mazda spectrum. Intensities were measured at the beginning and at the end of the experiment. These average values, together with the plant data for 3 weeks' growth are given in table 2.

TABLE 2.—Radiation intensities and average plant data from experiment 3

Culture nos.	Radiation intensity watts/cm ²				Average data per plant		
	Red	Blue	White	Total	Stem ht. cm	Root length cm	Total dry wt. gram
1 and 2.....	.0055	.00220057	6.3	38	.026
3 and 4.....	.0028	.00110039	7.4	50	.038
5 and 6.....0056	.0056	8.0	44	.028

The greatest amount of dry weight was produced by cultures 3 and 4, although the total light intensity was less than under the other two conditions of growth. Here the blue radiation was about 28 percent of the total. Although these data are meager, there is an indication that considerable differences in growth are obtained by manipulating the wave-length distribution as well as the total intensity.

Experiment 4.—In the next experiment wave-length distribution was further restricted by using neon and mercury grids as light sources. These were constructed in our laboratory by Mr. L. B. Clark. In order to increase the intensities a mirror was placed back of each. Three duplicate cultures were placed between these two light sources, each culture jar containing three tomato seedlings. This increased the number of plants per treatment to six. Because of reflections in the mirrors some red light came from the blue side and some blue light came from the red side of the cultures. As will be seen in table 3, the intensity of radiation was considerably less than in the earlier experiments. The plants were grown for 26 days

and then harvested. The average stem height and total dry weight per plant for each of the three light conditions appear in the same table.

Although the stems of plants in group 1-2 were thicker than those in the other groups, their leaves were quite yellow. Here again yellowing is associated with energy distribution where the greatest amount is found in the red end of the spectrum. The plants in group 5-6 had the best color, even though the total amount of energy was about half that of group 1-2. These leaves had flat smooth surfaces, while those in group 1-2 were quite pointed and curled. The general appearance of these plants is shown in plate 1. After another experiment with these lamps it was definitely indicated that the plants were getting insufficient illumination.

Experiment 5.—To increase the radiation, a General Electric 400-watt high-pressure mercury lamp was substituted for the mercury

TABLE 3.—*Radiation intensities and average plant data from experiment 4*

Culture no.	Radiation intensity at beginning of experiment watts/cm ²			Average data per plant	
	Neon (red)	Mercury (blue)	Total	Stem ht. cm	Total dry wt. gram
1.....	.00023	.00002	.00025	6.6	.029
2.....	.00019	.00002	.00021	6.6	.029
3.....	.00008	.00002	.00010	3.6	.014
4.....	.00008	.00002	.00010	3.6	.014
5.....	.00005	.00007	.00012	3.4	.013
6.....	.00005	.00007	.00012	3.4	.013

grid and four instead of two transformers were used with the neon lamp. The daily light period was increased from 12 hours to 18 hours. Because of the marked decrease in the life of the neon lamp under these forced conditions, the experiment was discontinued at the end of 20 days. In this exploratory experiment no accurate intensity measurements were made. However, general improvement in growth was noted.

Experiment 6.—To increase further the light intensity, a 1,000-watt, 110-volt projection lamp housed in a water jacket as noted earlier (experiment 1) was substituted for the neon grid lamp. Three plants per quart culture jar were used and the cultures run in duplicate so far as the light relations were concerned. Throughout all the previous experiments the plants were grown in a three-salt nutrient solution similar to that used by Johnston and Dore (1929). In this experiment cultures 2, 4, and 6 had $(\text{NH}_4)_2\text{SO}_4$ added to the former solution which contained $\text{Ca}(\text{NO}_3)_2$, MgSO_4 , and KH_2PO_4

and traces of Mn, B. Iron was added as FeSO_4 to all cultures from time to time as conditions demanded. Because the Mazda lamp was run at about its voltage limit its life was short, and replacements were necessary every 6 or 7 days. The plants were grown for 3 weeks with a daily light period of 18 hours. The added heat from the lamps caused a slight daily temperature fluctuation. The average maximum was 24°C . and the average minimum 21.5°C . This resulted in a change in humidity which averaged 57 and 51 percent for the dark and light periods respectively. As found in previous experiments, a temperature fluctuation is beneficial to the tomato plant. Better growth was obtained by subjecting the plants to a lower dark period

TABLE 4.—*Radiation measurements at beginning of experiment 6*

Culture nos.	Watts/cm ²			Foot-candles with small G. E. meter		
	Mazda	Mercury	Total	Mazda	Mercury	Total
1 and 2.....	.0404	.0013	.0417	2,800	200	3,000
3 and 4.....	.0172	.0031	.0203	1,200	600	1,800
5 and 6.....	.0065	.0067	.0132	550	1,000	1,550

TABLE 5.—*Plant data from experiment 6 expressed as averages per plant*

Culture no.	Stem ht. cm	Green wt. grams Tops	Dry wt. gram		
			Tops	Roots	Total
1.....	17.5	6.6	.529	.139	.668
2.....	21.1	7.8	.671	.174	.845
3.....	18.9	5.6	.463	.091	.554
4.....	20.9	6.1	.469	.074	.543
5.....	23.5	5.0	.384	.074	.458
6.....	23.8	5.4	.371	.057	.428

temperature (about 3°C . lower) than by maintaining a constant temperature during the dark and light periods.

The intensity measurements which were made at the beginning of the experiment are presented in table 4.

After 3 weeks of growth the plants were photographed (pl. 2) and harvested. Data giving average stem height, green weight of tops, and dry weight of tops and roots are given in table 5.

Both the illustrations and plant data show that this group of plants was normal in appearance and comparable to good greenhouse plants. It was by far the best we have grown under the 100 percent artificial conditions of our laboratory. In an earlier publication, Johnston (1932) reported that tomato plants exposed to an intense illumination from a Mazda lamp grew very well but soon became yellow in color.

The near infrared radiation was apparently destructive to chlorophyll or inhibited its formation. This again appeared to be the case for the three plants in culture 1. However, one of the most interesting observations made in this experiment was that the color of the plants in culture 2, which received the same radiation intensity as those of no. 1, was much greener. This color difference is seen to some extent in plate 2 as differences in light and dark tones of the plants in the upper and lower figures. This was also true for the plants in cultures 4 and 6, as compared with cultures 3 and 5 respectively, which were grown under similar light conditions. All the plants grown in nutrient solution to which $(\text{NH}_4)_2\text{SO}_4$ had been added were greener than the corresponding ones without this additional nitrogen. This observation suggests the influence of the type of radiation on the uptake of mineral nutrients. This same solution without the $(\text{NH}_4)_2\text{SO}_4$ has been used in growing tomato plants in the greenhouse but the characteristic chlorotic effects were not noted until the plants were grown under Mazda lamps.

The percentages of added mercury radiation to total illumination were 3, 15, and 50 respectively for cultures 1-2, 3-4, 5-6. The green color of the leaves was deeper where this percentage was larger. A more striking color difference occurred, however, between the plants in cultures with and without the $(\text{NH}_4)_2\text{SO}_4$.

The average total dry weight per plant for each of the three light conditions 1-2, 3-4, 5-6 was .757, .549, and .443 gram respectively. Under these three light conditions the efficiency in the production of dry weight per watt/cm² was 18, 27, and 34 respectively. Although the total intensity of 5-6 was about a third that of 1-2, on the basis of efficiency in producing dry weight per unit energy, the less intense radiation was about double that of the more intense.

One other factor in addition to wave-length distribution must be recognized in an experiment of this type. One lamp (Mazda) gave practically continuous illumination; the other (mercury, 60-cycle), a fluctuating illumination varying from a minimum considerably below the average to a maximum much greater than the average as determined by the thermocouple and photoelectric cell. McAlister (1937) clearly shows that a change in efficiency of carbon dioxide assimilation occurs with frequency of intermittency of illumination. Although it may be comparatively safe to compare the different cultures in any one experiment since the "flicker" effect is doubtless the same, it is impossible to compare results of experiments in which the light is continuous with those in which it is intermittent or with those in which it is half continuous and half intermittent.

Experiment 7.—An experiment varying a little from the one just described was next performed. In this, five cultures of tomato seedlings were placed around the Mazda lamp at positions which gave them approximately equal light intensities from this lamp. A sixth culture was located at a position where the Mazda intensity was about half that of the other cultures. The intensities of each of the two lamps for each culture of these plants are best seen in table 6.

After 18 days the plants were harvested and their dry weights determined. The plant data appear in tables 7 and 8.

TABLE 6.—*Radiation measurements¹ from experiment 7*

Culture no.	Watts/cm ²			Foot-candles with small G. E. meter		
	Mazda	Hg	Total	Mazda	Hg	Total
1.....	.0234	.0097	.0331	1,300	2,000	3,300
2.....	.0241	.0018	.0259	1,300	300	1,600
3.....	.0241	.0013	.0254	1,400	200	1,600
4.....	.0240	.0013	.0253	1,400	200	1,700
5.....	.0231	.0039	.0270	1,300	600	1,900
6.....	.0112	.0090	.0202	600	1,900	2,500

¹ Since the original Mazda lamp was replaced after 6 days, these measurements were made on the second lamp on the 10th day of the experiment.

TABLE 7.—*Stem height (cm) data from experiment 7*

Plant	Culture number					
	1	2	3	4	5	6
a	16.5	16.2	19.0	18.5	22.2	19.8
b	15.8	18.0	15.5	22.3	22.5	19.5
c	14.5	19.4	19.0	20.0	20.6	18.5
Av. ht. at harvest.....	15.6	17.9	17.8	20.3	21.8	19.3
Av. original ht.....	2.3	2.1	2.2	1.6	1.9	1.8
Av. increase in ht.....	13.3	15.8	15.6	18.7	19.9	17.5

TABLE 8.—*Average green and dry weights (grams) of plants from experiment 7*

Culture no.	Green wt. Tops	Dry wt.		
		Tops	Roots	Total
1.....	6.1	.713	.199	.912
2.....	4.2	.311	.044	.355
3.....	4.8	.391	.060	.451
4.....	5.8	.467	.064	.531
5.....	6.6	.582	.099	.681
6.....	6.3	.610	.145	.755

During the experiment water was added and fresh nutrient solution renewed as required. Because of frequent stopping of rotating table no. 1, these plants were slightly burned. These plants had the shortest internodes. Plants in culture 6 had next to the shortest internodes and were the best green. The leaves of plants in cultures 2, 3, 4, and 5 were slightly chlorotic. In order of their dry weights, plants in cultures 1, 6, and 5 were the best. It is interesting to compare the total dry weight per unit total energy with the percentage of energy received from the mercury lamp (table 9).

TABLE 9.—*Comparison of dry weight efficiency with amount of radiation from the mercury lamp*

Cultures	1	2	3	4	5	6
Ratio total dry wt. to watts/cm ²	27.6	13.7	17.8	21.0	25.2	37.4
Percentage radiation from mercury lamp....	29	7	5	5	14	45

Plants in cultures 6, 1, and 5 produced the greatest amount of dry weight per watt/cm². These same cultures in the order given received the largest percentages of radiant energy rich in the blue. Total energy (table 6) was greatest for culture 1 and least for culture 6. Cultures 2, 3, and 4 were practically equal. Thus, plants of culture 1 had the greatest total dry weight, and those of 6 were second. However, for greatest efficiency in the production of dry weight, plants in culture 6 were much better than those in culture 1. This is evidently related to the greater percentage of shorter wave length in the one case than in the other. When light intensity as measured by the foot-candle meter is considered, plants of culture 1 are shown as receiving the greatest amount of light and those of culture 2 the next greatest amount.

By consulting the table of stem heights it will be noted that the average height at harvest for plants in culture 1 was less than any of the other groups although the average original height was greatest. The least average stem elongation shown by this group may be correlated with the greatest amount of total energy received by these plants. But little difference in stem height is seen between plants of the other cultures. Likewise there is but little difference in total energy received by these same cultures. Other observations bear out this same point that an intense light retards stem elongation more than a less intense one. Although the shorter wave lengths have a greater retarding effect, this difference between plants of cultures 6 and 1 must have been offset by the differences in total radiation intensities.

Experiment 8.—In the last experiment of this series, the same types of lamps were used. Also each culture contained three tomato plants. The first four cultures (nos. 1, 2, 3, 4) were arranged around the mercury lamp at approximately equal distances. The other two (nos. 5 and 6), together with those numbered 3 and 4, were located about equal distances from the water-cooled 115-watt Mazda projection lamp. The intensity measurements taken at the beginning of the experiment are shown in table 10.

TABLE 10.—*Radiation measurements in experiment 8*

Culture no.	Intensity measurements					
	Watts/cm ²			Foot-candles		
	Mazda	Hg	Total	Mazda	Hg	Total
1.....	.0071	.0048	.0119	350	700	1,050
2.....	.0071	.0047	.0118	350	700	1,050
3.....	.0140	.0046	.0186	800	700	1,500
4.....	.0144	.0045	.0189	800	700	1,500
5.....	.0137	.0010	.0147	900	200	1,100
6.....	.0146	.0010	.0156	900	200	1,100

At the end of three weeks the plants were photographed and harvested. Since each culture of three plants was duplicated, the average of the six plants is shown in table 11.

TABLE 11.—*Plant data from experiment 8 expressed as averages per plant*

Culture nos.	Plant data expressed as averages per plant						
	Final stem ht. (cm)	No. of leaves	Green wt. of tops (g)	Total transpirational water loss (ml)	Dry weight (g)		
					Tops	Roots	Total
1 and 2....	18.3	6	3.5	157	.240	.042	.282
3 and 4....	20.8	7	6.1	251	.437	.097	.534
5 and 6....	15.8	5	2.6	98	.140	.021	.161

Plants of cultures 3-4 were best in general appearance and had the thickest stems. Those of cultures 5-6 were lightest green. Plants with longest roots were found in cultures 5-6; those with shortest roots occurred in cultures 1-2.

The general appearance of the cultures about the two lamps in this experiment may be seen in plate 3, and the appearance of the tops and roots of the plants at the end of the experiment is seen in plate 4.

It will be recalled that in experiment 6 the ratio of dry weight to total energy increased with the percentage of added radiation from the mercury lamp. Also in experiment 7, table 9, the three cultures

in which the greatest dry weight was produced per watt/cm² were the same three cultures which received the greatest percentage of radiation from the mercury lamp. In experiment 8, however, an exception occurred. The dry weight efficiencies for the three groups of cultures 1-2, 3-4, 5-6, were 23.8, 28.6, 10.7 respectively, while the percentages of total radiation attributed to the mercury lamp were 40, 25, and 7 for these same cultures in the order given. It is not clear from the data at hand why this exception occurred.

In order to compare all these data which are fairly comparable, table 12 has been constructed. Since two types of solutions were used in experiment 6, cultures 2, 4, and 6 were selected as their solutions

TABLE 12.—*Average dry weight production per unit total radiation (Mazda plus mercury lamp) in relation to percentage of radiation from the mercury lamp*

Experiment number	Culture number	Dry wt. per watt/cm ²	Percentage radiation from mercury lamp
7.....	6	37.4	45
8.....	3	32.7	25
6.....	6	32.4	51
8.....	1	28.2	40
7.....	1	27.6	29
6.....	4	26.8	15
7.....	5	25.2	14
8.....	4	24.4	24
7.....	4	21.0	5
6.....	2	20.3	3
8.....	2	19.4	40
7.....	3	17.8	5
7.....	2	13.7	7
8.....	6	11.0	6
8.....	5	10.3	7

were similar to those used in experiments 7 and 8. All plant values given in this table are the averages of three plants. There is a slight difference in the duration of the three experiments which should be kept in mind in making this comparison. In these experiments, 6, 7, and 8, the plants were grown for 20, 18, and 21 days respectively.

The data showing dry weight produced per unit total energy in table 12 have been arranged from greatest to least value. The corresponding values showing the percentages of total radiation that are obtained from the mercury lamp fall roughly into two groups. The first eight values are high (14 to 51 percent). The remaining seven with the exception of culture 2 in experiment 8 are low (3 to 7 percent). Although there is no regular decrease in these percentage values with the decrease in dry weight per unit total radiation, there

appears to be a general decrease in dry weight efficiency with illumination containing less of the shorter wave lengths found in the mercury lamp.

DISCUSSION

Plants have been grown by Harvey (1922), Hendricks and Harvey (1924), and others under Mazda lamps. Davis and Hoagland (1928), Arthur, Guthrie and Newell (1930), Garner and Allard (1931), Steinberg and Garner (1936), and others have conducted numerous experiments in which good growth was obtained with Mazda lamps for various lengths of daily light and dark periods. Many other investigators both in Europe and in this country have shown that plants may be grown in artificial light whose wave-length distribution is continuous from blue-violet to red. Other investigators have determined the growth of plants in different portions of the spectrum. Here it was necessary to use glass or liquid filters. Others, like Roodenburg (1932), have used gaseous discharge lamps such as neon. Most of these experiments indicate the necessity of the full visible spectrum for normal growth. Popp's (1926) results indicate that the blue-violet end of the spectrum is necessary for normal growth although the ultraviolet may not be indispensable. Shirley (1929) states that "The entire visible and ultra-violet solar spectrum is more efficient for the growth of the plants studied than any portion of it used; the blue region of the spectrum is more efficient than the red region." Schappelle (1936) concluded that white light is best for normal plant response. Either end of the visible spectrum without the other causes abnormal growth. Infrared, between 0.8μ and 2.0μ was ineffective in bringing about fruiting of *Marchantia*, while red and blue lights were of approximately equal effectiveness.

Arthur and Stewart (1935) made a comparison of the growth of buckwheat plants under Mazda, neon, sodium, and mercury vapor lamps. For short periods of 8 to 10 days the sodium lamp was found to be most efficient in the production of dry weight. No relation was found between the absorption bands of chlorophyll and the emission bands of the various lamps. These gaseous discharge lamps produced plants with greener leaves than the Mazda lamps. Later Arthur and Harvill (1937) show that the sodium lamp alone is not ideal for the continuous growth of plants over long periods of time. If, however, the continuous exposure from the sodium lamps is supplemented by an exposure of 2 hours per day from an 85-watt capillary mercury vapor lamp, excellent leaf color and flowering could be produced in

such plants as begonia, gardenia, cotton, geranium, buckwheat, and snapdragon. Although this light source was not satisfactory for the tomato plant, the authors point out that other wave bands of light may be found which should be added or subtracted for the best growth of some plants such as the tomato.

Dastur and Mehta (1935) determined the rate of photosynthesis in approximately equal intensities of red, blue, and white light. Photosynthetic activity was greatest in the white light, intermediate in the red light, and least in the blue light. They state that both the red and blue regions are necessary for normal photosynthesis.

Equally interesting are the results of Hoover's (1937) investigation on determining the rate of CO_2 absorption as a function of wave length on the basis of equal incident energy. The principal maximum occurred at 6500 Å in the red, and a secondary maximum came at 4400 Å in the blue. The greater transmission and reflection of radiation in the green region decreased the effectiveness in that portion of the spectrum. The limits of CO_2 absorption were placed between 7200 Å and 7500 Å in the red, and below 3650 Å in the blue end of the spectrum.

Dastur and Solomon (1937) show the importance of the blue-violet end of the spectrum in photosynthesis in a series of experiments in which plants are grown in the light of a carbon arc, in "mixed" light where the gas-filled electric lamp light has superimposed upon it a beam of blue-violet light, and in the light of the gas-filled electric lamp alone. The "mixed" light was composed of two beams originating in a single source (1,000-watt flood lamp) and reflected to the plant by mirrors. One beam was passed through a copper sulphate filter which limited the wave-length band to the region 4200 Å to 4720 Å. These beams (white and blue) were reunited in the proportion 1:1 on an intensity basis. Plants grown in these three lights showed greatest photosynthetic activity in the carbon arc light, intermediate in the "mixed" light, and least in the gas-filled electric bulb light. This follows the order of richness in blue-violet light of the three sources.

From the foregoing discussion it would appear that plants can be grown in artificial light, but for more or less normal growth the light should include those wave lengths found in the visible solar spectrum. An increase in intensity or the absence of a given portion of this spectrum brings about abnormal growth responses. Undoubtedly, the more nearly the artificial light resembles sunlight in its energy distribution, the more nearly normal are the plant growth responses.

In the experiments reported in the present paper, a method for mixing artificial lights was used, but one quite different from that used by the above-mentioned investigators. A beginning was made by using two light sources, one rich in red, the other rich in blue light. By locating the plants on small rotating tables at different distances from these light sources, practically any intensity ratio of the two could be obtained. With this general scheme the number of lights could be increased, thus making it possible to study the effects of any given mixture of restricted wave-length regions on the growth of plants. With each added light, however, the interpretation of data becomes more difficult. By using this method it is difficult to grow many duplicate individuals at one time, especially if they grow large. This objection may be met in part by repeating an experiment often enough to obtain more reliable statistical data.

The first two experiments with the Mazda light vs. the Mazda light filtered through a CuSO_4 solution were mostly exploratory in nature. There is some indication that the greatest dry weight produced is associated with wave-length distribution and not entirely correlated with intensity of radiation. Although the data of experiment 3 are meager, a considerable difference in growth was obtained between plants receiving different amounts of red (wave lengths longer than 6040 Å) and blue (wave lengths shorter than 6040 Å). The dry weight increase for the plants receiving red-blue light in the ratio 72:28 was about 40 percent over those receiving white light and those receiving a mixture in the proportion 96:4, although the total intensities of these two cultures were over 40 percent greater.

An attempt was made to change the type of red and blue light by the use of neon and mercury grids. In these experiments (nos. 4 and 5) it was found that the intensity of radiation was too low for good growth. This made it impossible to draw any definite conclusion regarding the proportion of red to blue that gave best growth. Yellowing or lack of greenness was associated with those light mixtures predominant in red.

In order to obtain lights of higher intensities, one rich in red, the other rich in blue, the water-jacketed projection Mazda lamp used in experiments 1 and 2 and the 400-watt high-pressure mercury lamp used in experiment 5 were employed. With this combination of lights very good growth was obtained under 100 percent artificial conditions. Because of this good growth and the increased number of plants per treatment, more weight can be attached to the data from experiments 6, 7, and 8, than to the earlier ones. Where light and not carbon

dioxide is the limiting factor, the dry weight increases with increased illumination. Hoover, Johnston, and Brackett (1933), working with wheat plants, found that in normal air CO_2 became limiting at a light intensity of about 0.05 to 0.06 watts/cm². In none of these experiments with the tomato plant was the intensity greater than these values. Although the two plants may not behave exactly alike, it is reasonable to suppose they are similar enough to assume that at no time was CO_2 the limiting growth factor. In order to accentuate growth differences due to wave-length mixtures and minimize the effect of intensity on dry weight production, the dry weight data were divided by watts/cm². This dry weight efficiency of comparable cultures in the last three experiments was used as a criterion of the effect short-wave (blue) radiation added to that of longer wave length had on plant growth. It would appear from the data given in table 12 that a greater amount of dry weight is produced with a Mazda light by enriching it with blue from a mercury lamp to the extent of 14 to 51 percent under the conditions of these experiments. Care should be exercised in drawing any far-reaching conclusions, for with a change in quality or wave-length distribution of the Mazda or other source rich in red, changes undoubtedly will be necessary in other portions of the spectrum. Although for good growth plants very probably tolerate a rather wide range in wave-length distribution, yet it would appear that the more nearly this distribution in artificial light approaches that of sunlight the better will the plants grow.

SUMMARY

Emphasis is placed on the importance of quality or wave-length distribution of light in affecting plant growth. A method and several experiments are described in which plants were grown in "mixed" lights. By placing the plants on small rotating tables between two light sources, one rich in red, the other rich in blue, the proportion of each type of radiation falling on each culture was varied by the position of the culture with reference to the light sources.

As found in previous experiments, yellowing of leaves occurred in light rich in near infrared. Since this trouble could be corrected to a considerable extent by the type of nutrient solution used, it indicates the importance of wave-length distribution on the uptake of mineral nutrients.

Excellent growth under entirely artificial conditions was obtained with plants grown between a 1,000-watt, water-jacketed, projection Mazda lamp and a 400-watt, high-pressure mercury lamp. The posi-

tions of the plants for good growth were such that from 14 to 51 percent of the total radiation falling on them came from the mercury lamp. In several cases better growth was attained in one mixture of wave-lengths than in another where the total intensity was higher. However, the relatively high growth efficiency may in part be due to an intermittency effect occurring in gaseous discharge tubes such as the mercury lamp here used.

LITERATURE CITED

- ARTHUR, JOHN M., GUTHRIE, JOHN D., and NEWELL, JOHN M.
1930. Some effects of artificial climates on the growth and chemical composition of plants. *Amer. Journ. Bot.*, vol. 17, pp. 416-482.
- ARTHUR, JOHN M., and HARVILL, EDWARD K.
1937. Plant growth under continuous illumination from sodium vapor lamps supplemented by mercury arc lamps. *Contr. Boyce Thompson Inst.*, vol. 8, no. 5, pp. 433-443.
- ARTHUR, JOHN M., and STEWART, W. D.
1935. Relative growth and dry weight production of plant tissue under Mazda, neon, sodium and mercury vapor lamps. *Contr. Boyce Thompson Inst.*, vol. 7, no. 2, pp. 119-130.
- DASTUR, R. H., and MEHTA, R. J.
1935. The study of the effect of blue-violet rays on photosynthesis. *Ann. Bot.*, vol. 49, no. 196, pp. 809-821.
- DASTUR, R. H., and SOLOMON, S.
1937. A study of the effect of blue-violet rays on the formation of carbohydrates in leaves. *Ann. Bot.*, n. s., vol. 1, no. 1, pp. 147-152.
- DAVIS, A. R., and HOAGLAND, D. R.
1928. An apparatus for the growth of plants in a controlled environment. *Plant Physiol.*, vol. 3, no. 3, pp. 277-292.
- GARNER, W. W., and ALLARD, H. A.
1931. Effect of abnormally long and short alternations of light and darkness on growth and development of plants. *Journ. Agr. Res.*, vol. 42, no. 10, pp. 645-651.
- HARVEY, R. B.
1922. Growth of plants in artificial light. *Bot. Gaz.*, vol. 74, no. 4, pp. 447-451.
- HENDRICKS, ESTEN, and HARVEY, R. B.
1924. Growth of plants in artificial light required for blooming. *Bot. Gaz.*, vol. 77, pp. 330-334.
- HOOVER, W. H.
1937. The dependence of carbon dioxide assimilation in a higher plant on wave length of radiation. *Smithsonian Misc. Coll.*, vol. 95, no. 21, pp. 1-13.
- HOOVER, W. H., JOHNSTON, EARL S., and BRACKETT, F. S.
1933. Carbon dioxide assimilation in a higher plant. *Smithsonian Misc. Coll.*, vol. 87, no. 16, pp. 1-19.

JOHNSTON, EARL S.

1932. The functions of radiation in the physiology of plants. II. Some effects of near infra-red radiation on plants. *Smithsonian Misc. Coll.*, vol. 87, no. 14, pp. 1-15.

JOHNSTON, EARL S., and DORE, W. H.

1929. The influence of boron on the chemical composition and growth of the tomato plant. *Plant Physiol.*, vol. 4, pp. 31-62.

MCALISTER, E. D.

1937. Time course of photosynthesis for a higher plant. *Smithsonian Misc. Coll.*, vol. 95, no. 24, pp. 1-17.

POPP, HENRY WILLIAM.

1926. A physiological study of the effect of light of various ranges of wave length on the growth of plants. *Amer. Journ. Bot.*, vol. 13, pp. 706-736

ROODENBURG, J. W. M.

1932. *Kunstlichtcultuur*. II. Over de noodzakelijke van planten en neonbelichting bij bloemcultures. *Med. Wagen. (Nederland)*, vol. 36, no. 2, pp. 1-37.

SCHAPPELLE, N. A.

1929. Effect of narrow ranges of wave-lengths of radiant energy, and other factors, on the reproductive growth of long-day and short-day plants. *Cornell Univ. Agr. Exp. Stat. Mem.* 185, pp. 1-33.

SHIRLEY, HARDY L.

1929. The influence of light intensity and light quality upon the growth of plants. *Amer. Journ. Bot.*, vol. 16, pp. 354-390.

STEINBERG, ROBERT A., and GARNER, W. W.

1936. Response of certain plants to length of day and temperature under controlled conditions. *Journ. Agr. Res.*, vol. 52, no. 12, pp. 943-960.

EXPLANATION OF PLATES

PLATE I

Tomato plants grown for 26 days under the following intensities (watts/cm²). Daily illumination was 12 hours.

Culture	Neon	Mercury
1.....	.00023	.00002
3.....	.00008	.00002
5.....	.00005	.00007

PLATE 2

Tomato plants grown for 21 days under the following intensities (watts/cm²). Daily illumination was 18 hours.

Culture	Mazda (water-cooled)	Mercury (400 watt)
1 and 2.....	.0404	.0013
3 and 4.....	.0172	.0031
5 and 6.....	.0065	.0067

The darker green leaves in cultures 2, 4, and 6, due to the added (NH₄)SO₄, appear in the illustrations as a deeper shade than those in cultures 1, 3, and 5.

PLATE 3

General arrangement of cultures in experiment 8 on rotating tables placed about the two light sources. The Mazda lamp encased in a water jacket is on the left and the 400-watt mercury lamp on the right. The small rotating tables turned at the rate of 3.4 r.p.m. This prevented phototropic curvature of the stems but not of the leaves which, although turgid, appear wilted.

PLATE 4

Tomato plants grown for 21 days under the following intensities (watts/cm²). Daily illumination was 18 hours.

Culture	Mazda (water-cooled)	Mercury (400 watts)
1.....	.0071	.0048
2.....	.0071	.0047
3.....	.0140	.0046
4.....	.0144	.0045
5.....	.0137	.0010
6.....	.0146	.0010



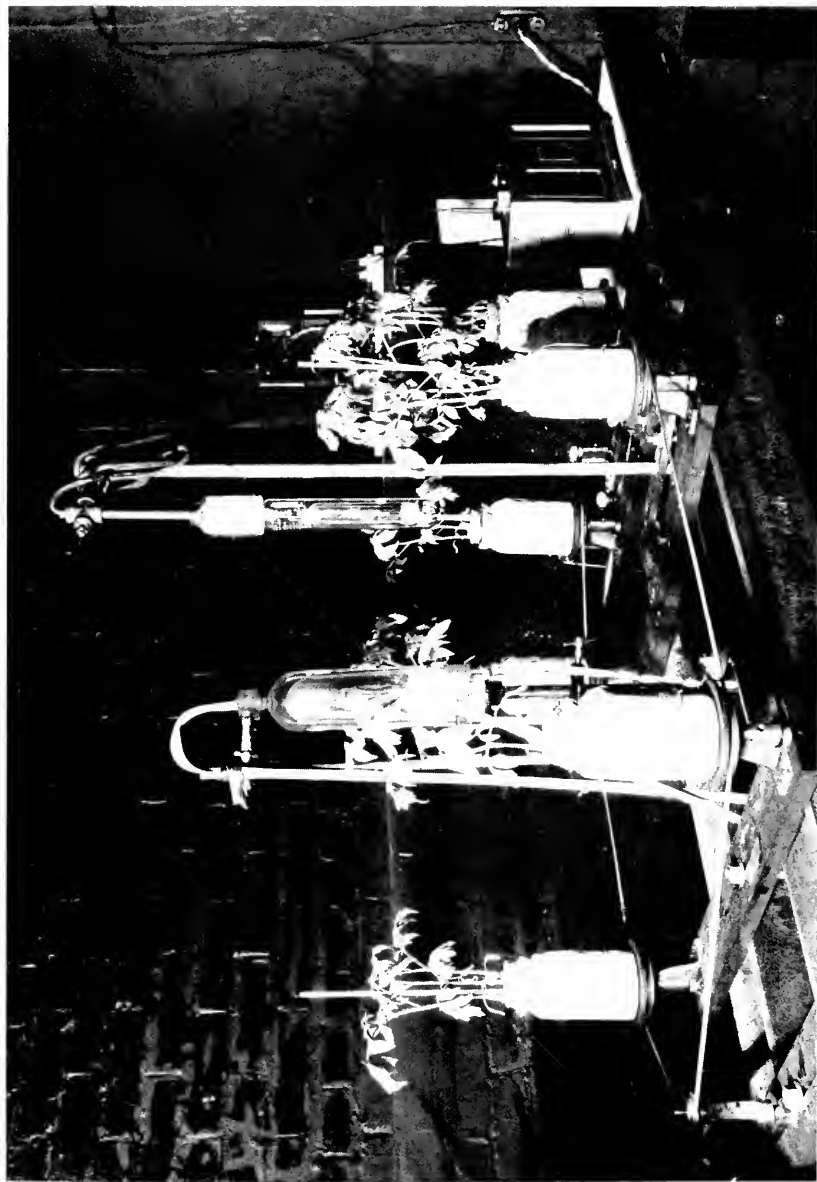
GENERAL APPEARANCE OF TOMATO PLANTS IN EXPERIMENT 4, GROWN BETWEEN MERCURY
AND NEON LAMPS

(For explanation, see pages 4 and 17.)

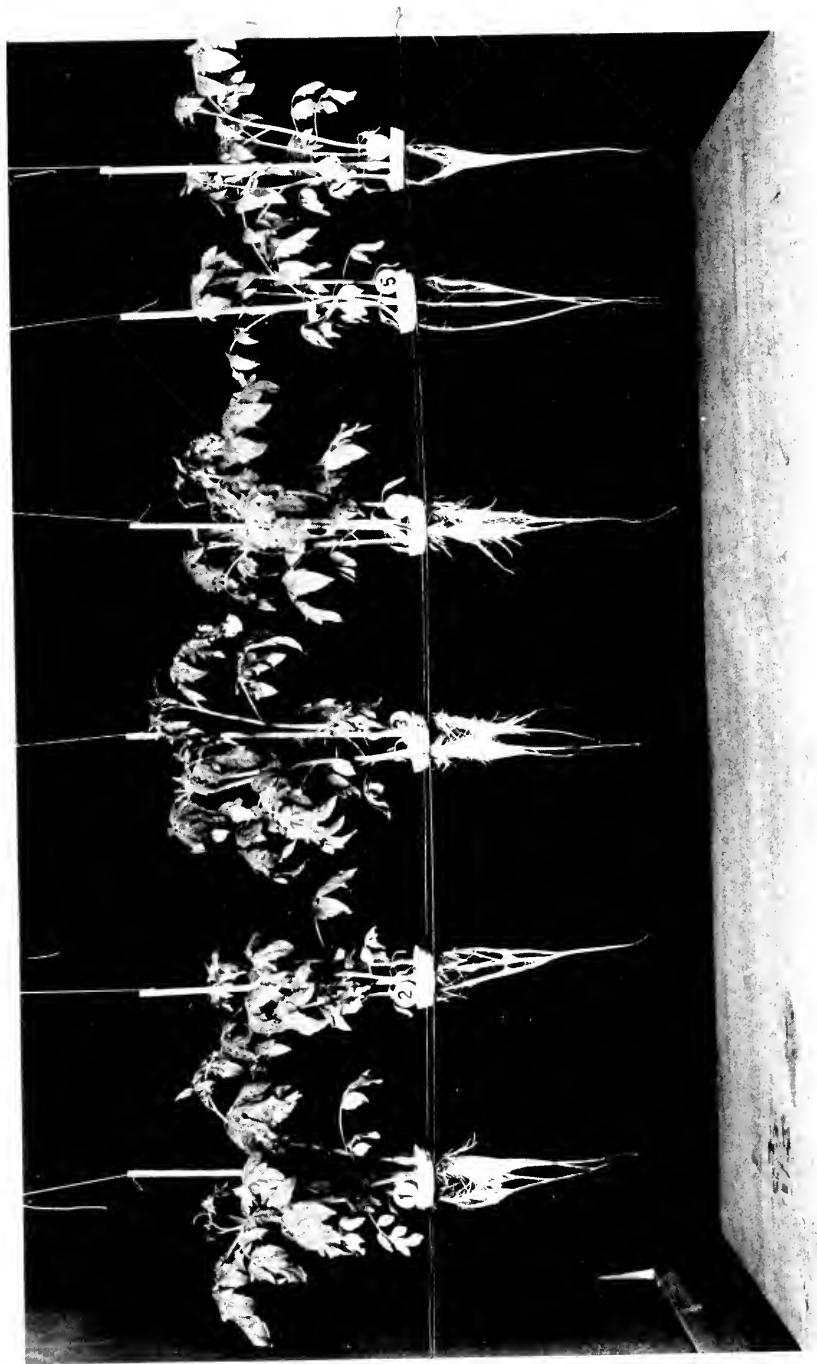


GENERAL APPEARANCE OF PLANTS IN EXPERIMENT 6. GROWN BETWEEN
MAZDA AND MERCURY LAMPS

(For explanation, see pages 5 and 17.)

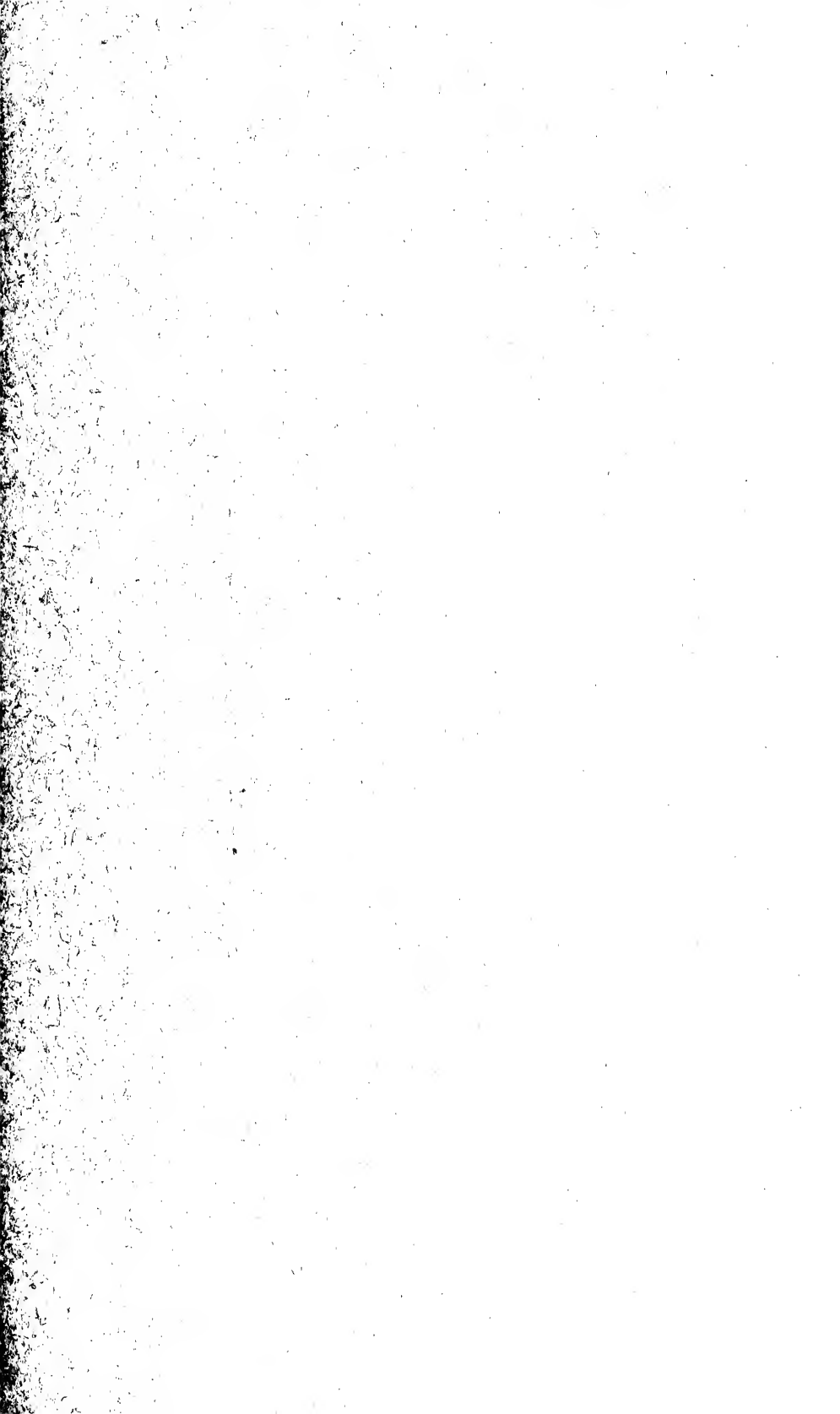


GENERAL ARRANGEMENT OF CULTURES IN EXPERIMENT 8. ON ROTATING TABLES. PLACED AT DIFFERENT DISTANCES FROM THE TWO LIGHT SOURCES
(For explanation, see pages 16 and 18.)



GENERAL APPEARANCE OF PLANTS AT THE CONCLUSION OF EXPERIMENT 8

(For explanation, see pages 10 and 18.)





SMITHSONIAN MISCELLANEOUS COLLECTIONS
VOLUME 97, NUMBER 3

MIDDLE CAMBRIAN FOSSILS FROM PEND OREILLE LAKE, IDAHO

(WITH ONE PLATE)

BY
CHARLES ELMER RESSER
Curator, Division of Invertebrate Paleontology,
U. S. National Museum



(PUBLICATION 3447)

CITY OF WASHINGTON
PUBLISHED BY THE SMITHSONIAN INSTITUTION
JANUARY 3, 1938

SMITHSONIAN MISCELLANEOUS COLLECTIONS
VOLUME 97, NUMBER 3

MIDDLE CAMBRIAN FOSSILS FROM PEND OREILLE LAKE, IDAHO

(WITH ONE PLATE)

BY
CHARLES ELMER RESSER
Curator, Division of Invertebrate Paleontology,
U. S. National Museum



(PUBLICATION 3447)

CITY OF WASHINGTON
PUBLISHED BY THE SMITHSONIAN INSTITUTION
JANUARY 3, 1938

The Lord Baltimore Press
BALTIMORE, MD., U. S. A.

MIDDLE CAMBRIAN FOSSILS FROM PEND OREILLE LAKE, IDAHO

By CHARLES ELMER RESSER

Curator, Division of Stratigraphic Paleontology

U. S. National Museum

(WITH ONE PLATE)

INTRODUCTION

From 1921 to 1924 Dr. Edward Sampson, of Princeton University, then a member of the United States Geological Survey, examined the Pend Oreille mining district which surrounds the southern part of Pend Oreille Lake, Bonner County, Idaho. A fossiliferous Middle Cambrian series crops out in several of the fault blocks into which the district is divided. This was the first Cambrian outcrop discovered in that part of North America. Subsequently, other Cambrian areas were found in the northwestern United States and the adjacent portions of Canada, in the extensive area previously thought barren of Cambrian strata except for the occurrence in the Lewis and Clark Range, west-central Montana. These occurrences were briefly discussed in 1934.¹ Since the Pend Oreille Lake area is isolated from other Cambrian outcrops and the stratigraphic succession is clearly determined, description of the faunas is desirable.

Dr. Sampson published a brief summary² of his findings in the district and described the stratigraphy, naming three Cambrian formations.

BELTIAN

Before discussing the Middle Cambrian formations a few words descriptive of the underlying Beltian strata are in order. Five Beltian formations, totaling more than 30,000 feet, are described beneath the Middle Cambrian. This enormous thickness of sediments consists of argillaceous sandstone, fine-grained massive sandstone, and heterogeneous beds of quartzite, sandstone, and argillite, with or without a

¹ Resser, C. E., Recent discoveries of Cambrian beds in the northwestern United States. *Smithsonian Misc. Coll.*, vol. 92, no. 10, 1934.

² Sampson, Edward, Geology and silver ore deposits of the Pend Oreille District, Idaho. *Idaho Bur. Mines Geol.*, Pamphlet 31 (mimeographed), 1928.

calcareous content. Cross-bedding, sun cracks, ripple marks and the other usual Beltian features characterize the series, but contemporaneous igneous rocks are evidently lacking, which is also the case in the Beltian strata of nearby western Montana.

MIDDLE CAMBRIAN

The Middle Cambrian series of the Pend Oreille region begins with a quartzite, which is followed in turn by argillaceous shale and calcareous formations. No mention is made of younger strata, and the published structure sections indicate that the Cambrian is not overlain by other beds.

Gold Creek quartzite.—The Gold Creek quartzite, which is estimated to average 400 feet in thickness, is easily distinguished from the Beltian by its coarser grain. Some of the conglomeratic beds contain pebbles up to 3 inches in diameter and cross-bedding is a characteristic feature. Outcrops are conspicuous because of the resistance of the rock to weathering. Unfortunately, the contact of the Gold Creek with the Beltian rocks is not clearly exposed so that essential history is lacking.

Rennie shale.—This formation is only 50 to 75 feet thick and consists of soft olive argillaceous shale, sometimes micaceous. Because it is so easily eroded, the Rennie shale seldom crops out. In fact, the fossils here described were collected from the bed of a brook.

The published summary fails to mention the fossiliferous limestone nodules present in the Rennie shale. They evidently are about the same size and shape as similar nodules obtainable from most Cambrian shales in the Cordilleran region. Internally, however, these nodules are peculiar as they consist of an odd mixture of brown and blue limestone. Both sorts occur as distinct masses, sometimes sharply angular, but more frequently irregular in shape, and the change from one to the other is abrupt. The brown limestone, which looks like a fine sandstone, is evidently rather pure calcium carbonate, judging from its rapid effervescence, and, since this portion of the rock does not scratch steel, it is assumed to be free from silica or sand. On the other hand, the blue limestone masses contain sand grains or silica, even though they also effervesce freely. Fossils are absent from the brown masses but are very abundant in the blue portions. Strangely, there are but two species of trilobites in these nodules, the abundant *Vanuxemella idahocnsis* and rare examples of *Albertella sampsoni*. Neither species has been recognized in the larger shale fauna, although elsewhere these trilobite forms are found together.

The shale has the species listed below. Besides the names given in this list there is a poor specimen that seems to be *Ecystites*. A few imperfect specimens of *Obolus* and a fragment of a shell similar to *Westonia ella* represent the brachiopods.

<i>Elrathia sampsoni</i> Resser	<i>Margaretia angustata</i> Resser
<i>Elrathia longiceps</i> Resser	<i>Schistometopus typicalis</i> Resser
<i>Glossopleura intermedia</i> Resser	<i>Urotheca sampsoni</i> Resser
<i>Hyolithes idahoensis</i> Resser	

Lakeview limestone.—Where unaltered, two rock types characterize this conspicuous and commercially valuable formation. One type consists of cliff-forming massive beds which vary from nearly pure limestone to nearly pure dolomite. The other beds are shaly, containing thin-bedded, highly fossiliferous limestone. Sampson does not state what relative position the two types hold with respect to each other, but the thin-bedded and shaly material probably forms the lower portion of the formation. Metamorphism caused different degrees of alteration, some of the beds becoming a crystalline marble.

Black crystalline limestone from the shaly beds yields an abundant fauna which is listed below.

<i>Acrothele speciosa</i> Resser	<i>Clavaspidella minor</i> Resser
<i>Acrotreta nitens</i> Resser	<i>Elrathia idahoensis</i> Resser
<i>Agnostus bommerensis</i> Resser	<i>Iphidella</i> cf. <i>pammula</i> (White)
<i>Alokistocare noduliferum</i> Resser	<i>Lingulella idahoensis</i> Resser
<i>Alokistocare natale</i> Resser	<i>Pagetia fossula</i> Resser
<i>Alokistocare nactum</i> Resser	<i>Oryctoccephalus walcotti</i> Resser
<i>Alokistocare notatum</i> Resser	<i>Utia curio</i> Walcott
<i>Alokistocare normale</i> Resser	<i>Zacanthoides sampsoni</i> Resser
<i>Alokistocare nothum</i> Resser	

A small collection of altered rock, presumably from the Lakeview formation, contains a pygidium of *Glossopleura*. Another lot of impure dark blue limestone is especially interesting because it contains, among other fossils, a species of *Tonkinella*, unfortunately too poorly preserved to illustrate. This is not the *Tonkinella*-like form described below as the pygidium possibly belonging to *Utia*.

RELATIONSHIP OF THE FAUNAS

It has already been pointed out that the faunas of the Rennie shale, both in the limestone nodules and in the shale, have no species in common. Nevertheless, both must be regarded as one fauna, since elsewhere they occur together. Neither have any species been found common between the Rennie shale and the Lakeview limestone. These faunas also are elsewhere found intermingled. From these facts it

seems that these faunas represent faunal subzones or possibly facies developments, but for purposes of correlation it is necessary to treat the faunas of the Rennie and Lakeview formations as a unit.

The fossils in the Rennie shale are clearly related to those in the Stephen formation.³ *Margaretia*, *Elrathia*, *Glossopleura*, and the particular form of *Hyolithes* are definite relatives of species in the Stephen. On the other hand *Vanuxemella* and *Albertella* are more characteristic of the older Ptarmigan formation of the Canadian Rockies. The Lakeview is also related to the Stephen, particularly by the *Agnostus*, *Oryctocephalus*, and *Zacanthoides*. The numerous species of *Alohistocare* are found more commonly in other Middle Cambrian formations than in the Stephen.

Close connection exists between the Lakeview and the Spence shale⁴ of southern Idaho. *Pagetia* and the rare trilobite *Utia curio* indicate that these two formations are identical in age. The other genera, both in the Lakeview and in the Rennie, occur in the Spence also.

DESCRIPTION OF THE FOSSILS

The identifiable material is described and illustrated as completely as possible. In order to avoid unnecessary printing, locality numbers are given with the descriptions and in the plate legend. A full description of the two localities is given below.

Locality 37m: Middle Cambrian, Rennie shale; headwaters North Gold Creek, south side of Packsaddle Mountain, east of Pend Oreille Lake, Idaho.

Locality 37n: Middle Cambrian, Lakeview limestone; cement mine just north of Lakeview, Pend Oreille Lake, Idaho.

MARGARETIA Walcott, 1931

MARGARETIA ANGUSTATA, n. sp.

Plate 1, fig. 2

A number of narrow flexible tubes have a surface roughened by elongate depressions typical of *Margaretia*. Compared with the genotype, *M. dorus*, as well as species in process of publication, *M. angustata* is considerably smaller in size, averaging less than one-fourth the diameter of the smaller specimens of the other species.

Locality 37m.

Holotype.—U.S.N.M. no. 95019.

³ Walcott, C. D., Mount Stephen rocks and fossils. Canadian Alpine Journ., vol. 1, no. 2, 1908.

⁴ Walcott, C. D., Smithsonian Misc. Coll., vol. 53, no. 1, p. 8, 1908.

UROTHECA Matthew, 1899**UROTHECA SAMPSONI**, n. sp.

Plate 1, fig. 1

Long, slender tubes abundant in the Rennie shale are referable to this genus. The illustrated specimen appears to have a carina but is merely broken in the middle. Faint annulations seem to occur on some individuals.

Locality 37m.

Holotype.—U.S.N.M. no. 95020.**HYOLITHES** Eichwald, 1840**HYOLITHES IDAHOENSIS**, n. sp.

Plate 1, figs. 57, 58

A species of *Hyolithes* occurs in the shale; unfortunately, most of the specimens are poorly preserved. The species is evidently related to *H. carinata* but is larger, the carina is less pronounced, and the operculum has wider wings.

Locality 37m.

Cotypes.—U.S.N.M. no. 95021.**LINGULELLA** Salter, 1866**LINGULELLA IDAHOENSIS**, n. sp.

Plate 1, fig. 18

This shell is nearest to *L. isse* in shape, but it is a smaller brachiopod. It is possible that this brachiopod is one of the Middle Cambrian forms now included in *L. desiderata*.

Locality 37n.

Holotype.—U.S.N.M. no. 95022.**ACROTHELE** Linnarsson, 1876**ACROTHELE SPECIOSA**, n. sp.

Plate 1, figs. 6, 7

This form is most like *A. colleni*, from which it differs in having weaker ribs and growth lines, but more particularly in the narrowness of the false area.

Locality 37n.

Cotypes.—U.S.N.M. no. 95023.

ACROTRETA Kutorga, 1847**ACROTRETA NITENS**, n. sp.

Plate 1, figs. 3-5

The generic reference is not certain, for this species differs from all described forms of *Acrotreta*. Recently, similarly constructed species have been found in both Lower and Middle Cambrian collections. The illustrations present clearly the characteristics of the species.

Locality 37n.

Cotypes.—U.S.N.M. no. 95024.**AGNOSTUS** Brongniart, 1822**AGNOSTUS BONNERENSIS**, n. sp.

Plate 1, figs. 16, 17

This agnostid is a typical form of the Cordilleran Middle Cambrian. The characteristic features place it between *A. montis* Matthew of the Stephen formation and *A. interstrictus* White from the Wheeler shale of Utah. *A. bonnerensis* has also been compared with the undescribed species in the Spence shale fauna, from which it differs in possessing axial furrows on the pygidium.

Locality 37n.

Holotype and paratypes.—U.S.N.M. no. 95025.**PAGETIA** Walcott, 1916**PAGETIA FOSSULA**, n. sp.

Plate 1, figs. 8-11

P. fossula is similar to *P. clytia* from the Spence shale, but differs in having a median furrow like *P. bootes*. The pygidium has short axial spines.

Locality 37n.

Cotypes.—U.S.N.M. no. 95026.**ALBERTELLA** Walcott, 1908**ALBERTELLA SAMPSONI**, n. sp.

Plate 1, figs. 24-26

The glabella of this species is long and is not expanded much in front. The pygidium is wide, much like *A. helena* and has a rather wide concave border, with a nearly straight posterior margin. The spines diverge more than average.

Locality 37m.

Holotype and paratypes.—U.S.N.M. no. 95027.

ALOKISTOCARE Lorenz, 1906**ALOKISTOCARE NORMALE, n. sp.**

Plate 1, fig. 14

This species is much like *A. subcoronatum* except for its larger size. Also the furrows, eyelines, and distribution of relief in the brim are different.

Locality 37n.

Holotype.—U.S.N.M. no. 95028.**ALOKISTOCARE NODULIFERUM, n. sp.**

Plate 1, figs. 52, 54

This species has a wide brim, the test is finely and closely granulated, the brim is striated beneath the test, and two nodes are situated in the dorsal furrow a short distance forward of the occipital furrow.

Locality 37n.

Holotype and paratype.—U.S.N.M. no. 95029.**ALOKISTOCARE NATALE, n. sp.**

Plate 1, fig. 53

A. natale is nearest like *A. noduliferum*. It has a brim of about the same size, and other proportions are similar. Small nodes are also present in the rear portion of the dorsal furrow. However, the surface of *A. natale*, which is finely granulated, has, in addition, scattered larger granules.

Locality 37n.

Holotype.—U.S.N.M. no. 95030.**ALOKISTOCARE NACTUM, n. sp.**

Plate 1, figs. 41, 42

A. nactum is characterized by a medium brim, on which a rather wide flat rim is differentiated by its upturned position.

Locality 37n.

Holotype and paratype.—U.S.N.M. no. 95032.**ALOKISTOCARE NOTHUM, n. sp.**

Plate 1, figs. 51, 55

This species is more normal than *A. nactum*, which it resembles. A medium swelling causes the rim to be less even in width throughout.

Locality 37n.

Holotype and paratype.—U.S.N.M. no. 95031.

AŁOKISTOCARE NOTATUM, n. sp.

Plate 1, fig. 43

This species departs considerably from the norm of the genus because of its convexity. The test is finely granulated, and only a narrow rim is differentiated by the upturned edge.

Locality 37n.

Holotype.—U.S.N.M. no. 95033.**ELRATHIA Walcott, 1924****ELRATHIA IDAHOENSIS, n. sp.**

Plate 1, figs. 36-40

A fullness in all parts of the cranium characterizes this species. It is typical of the genus in all respects. The thorax has about 15 segments.

Locality 37n.

Holotype and paratypes.—U.S.N.M. no. 95034.**ELRATHIA SAMPSONI, n. sp.**

Plate 1, figs. 31, 35, 58

Several crania of various sizes are illustrated, thus presenting the characteristics of the species. Compared with *E. idahoensis*, the species is somewhat narrower at the eyes, and the glabella is also tapered more.

Locality 37m.

Holotype and paratypes.—U.S.N.M. no. 95035.**ELRATHIA LONGICEPS, n. sp.**

Plate 1, fig. 50

Compared with *E. sampsoni*, this species has a longer glabella and relatively shorter brim; also, the brim is divided more nearly equally between the rim and preglabellar area.

Locality 37m.

Holotype.—U.S.N.M. no. 95036.**GLOSSOPLEURA Poulsen, 1927****GLOSSOPLEURA INTERMEDIA, n. sp.**

Plate 1, fig. 56

Several pygidia, librigenes, and two incomplete hypostomata, but no crania, were found in the shale collections. One pygidium is

figured. It is more like *G. boccar* than the Spence shale form because the doublure is not so wide. Fusion is carried nearly to the extinction of the rib furrows.

Locality 37n.

Holotype.—U.S.N.M. no. 95037.

ORYCTOCEPHALUS Walcott, 1886

ORYCTOCEPHALUS WALCOTTI, n. sp.

Plate I, figs. 22, 23

A small fragmentary granulated cranidium, with a typical *Oryctocephalus* glabella is tentatively referred to the species.

The pygidium is nearest like *O. reynoldsi*, differing in having heavier spines and more clearly impressed pleural grooves.

Locality 37n.

Holotype and paratype.—U.S.N.M. no. 95038.

CLAVASPIDELLA Poulsen, 1927

CLAVASPIDELLA MINOR, n. sp.

Plate I, figs. 45, 49

A number of specimens in the Lakeview limestone evidently belong to *Clavaspidella*. This species is much smaller than any other thus far described; also, both the pygidial axis and the eye lobes are long.

Locality 37n.

Holotype and paratypes.—U.S.N.M. no. 95039.

UTIA Walcott, 1924

UTIA CURIO Walcott

Plate I, figs. 19-21

Specific differences are not apparent between the *Utia* of the Lakeview limestone and of the Spence shale, consequently the Idaho form is identified as *U. curio*.

A peculiar small pygidium characterized by its radiating furrows and grooves is tentatively assigned to the species.

Locality 37n.

*Plesiotype*s. —U.S.N.M. no. 95041.

VANUXEMELLA Walcott, 1908

VANUXEMELLA IDAHOENSIS, n. sp.

Plate I, figs. 13-15

This species has stronger pygidial furrows than *V. nortia*, and also larger rear spines. Comparison with the Montana species, *V. con-*

tracta, shows that *V. idahoensis* has the rear spines set wider apart, giving the entire pygidium a wider aspect. *V. idahoensis* has incompletely fused pleural furrows.

Locality 37m.

Cotypes.—U.S.N.M. no. 95042.

SCHISTOMETOPUS, n. gen.

Diagnosis.—Glabella long, occupying nearly the entire cranial length; tapered slightly. There are four pairs of glabellar furrows and the occipital furrow. Fixigenes about half width of glabella. Anterior suture slightly divergent. Posterolateral limbs rather short. Eyes small, situated slightly behind the midpoint. Eyelines curved backward, arising opposite anterior pair of glabellar furrows. Brim consists of rim only. Two deep furrows run forward from the anterior angles of the dorsal furrow and separate a central thickened portion from the two flat lateral portions of the rim.

Genotype.—*S. typicalis*, new species.

Name.—σχιωπος = divided: μετωπος = forehead.

SCHISTOMETOPUS TYPICALIS, n. sp.

Plate 1, fig. 12

During preparation the important rim was injured because the specimen was thought to be an *Elrathia*. Fortunately, enough of the rim remains to show its features. It will be observed that the glabella of *S. typicalis* is like that of *Elrathia sampsoni* because of the four sets of furrows.

Locality 37m.

Holotype.—U.S.N.M. no. 95040.

ZACANTHOIDES Walcott, 1888

ZACANTHOIDES SAMPSONI, n. sp.

Plate 1, figs. 27-30

A small form of *Zacanthoides* is present in the Lakeview limestone. The pygidium has spines of nearly equal length, and the thorax has 8 or 9 segments. Glabellar furrows are short and shallow.

Locality 37n.

Holotype and paratypes.—U.S.N.M. no. 95043.

EXPLANATION OF PLATE

	PAGE
FIG. 1. <i>Urotheca sampsoni</i> , new species.....	5
Portion of a specimen. Holotype, $\times 2$.	
FIG. 2. <i>Margaretia angustata</i> , new species.....	4
Portion of the holotype, $\times 2$. Top portion is of the outside; lower portion, the impression.	
FIGS. 3-5. <i>Acrotreta nitens</i> , new species.....	6
3, 4. Ventral valves, $\times 4$.	
5. Dorsal valve, $\times 4$.	
FIGS. 6, 7. <i>Acrothele speciosa</i> , new species.....	5
Two ventral valves, $\times 2$.	
FIGS. 8-11. <i>Pagetia fossula</i> , new species.....	6
8, 11. Cranidia, $\times 4$.	
9, 10. Pygidia and a good cranidium, $\times 4$.	
FIG. 12. <i>Schistometopus typicalis</i> , new species.....	10
Holotype cranidium.	
FIGS. 13-15. <i>Vanuxemella idahoensis</i> , new species.....	9
13. A cranidium.	
14. Pygidium showing the spines.	
15. Cranidia and pygidium.	
FIGS. 16, 17. <i>Agnostus bonnerensis</i> , new species.....	6
16. A good cranidium, $\times 4$.	
17. Holotype pygidium, $\times 4$.	
FIG. 18. <i>Lingulella idahoensis</i> , new species.....	5
Interior of a ventral valve, $\times 4$.	
FIGS. 19-21. <i>Utia curio</i> Walcott.....	9
19, 20. Cranidia.	
21. Pygidium referred to the species, $\times 4$.	
FIGS. 22, 23. <i>Oryctocephalus walcotti</i> , new species.....	9
22. Cranidium referred to the species, $\times 4$.	
23. Holotype pygidium.	
FIGS. 24-26. <i>Albertella sampsoni</i> , new species.....	6
24, 25. Two cranidia.	
26. Holotype pygidium.	
FIGS. 27-30. <i>Zacanthoides sampsoni</i> , new species.....	10
27. A small cranidium, $\times 4$.	
28. The holotype.	
29. A large pygidium.	
30. A small cranidium, $\times 2$.	
FIGS. 31-35. <i>Elrathia sampsoni</i> , new species.....	8
31, 32, 35. Cranidia of various sizes.	
33. Holotype cranidium (see also fig. 58).	
34. Libragene.	
FIGS. 36-40. <i>Elrathia idahoensis</i> , new species.....	8
36-38. Cranidia of several sizes.	
39. Holotype cranidium, $\times 2$.	
40. Entire individual.	

	PAGE
FIGS. 41, 42. <i>Alokistocare nactum</i> , new species.....	7
41. Cranidium with librargene, $\times 2$.	.
42. Holotype cranidium, $\times 2$.	.
FIG. 43. <i>Alokistocare notatum</i> , new species.....	8
Holotype cranidium.	.
FIG. 44. <i>Alokistocare normale</i> , new species.....	7
Holotype cranidium.	.
FIGS. 45-49. <i>Clavaspidella minor</i> , new species.....	9
45. A small cranidium, $\times 2$.	.
46. Holotype cranidium, $\times 2$.	.
47. Librargene, $\times 2$.	.
48. A pygidium, $\times 4$.	.
49. A pygidium, $\times 2$.	.
FIG. 50. <i>Elrathia longicaps</i> , new species.....	8
Holotype cranidium.	.
FIGS. 51, 55. <i>Alokistocare nothum</i> , new species.....	7
51. Holotype cranidium, $\times 2$.	.
55. Partially exfoliated cranidium, $\times 2$.	.
FIGS. 52, 54. <i>Alokistocare noduliferum</i> , new species.....	7
52. Holotype cranidium.	.
54. A small cranidium.	.
FIG. 53. <i>Alokistocare natale</i> , new species.....	7
Holotype cranidium, $\times 2$.	.
FIG. 56. <i>Glossopleura intermedia</i> , new species.....	8
Holotype pygidium.	.
FIGS. 57, 58. <i>Hyolithes idahoensis</i> , new species.....	5
57. Operculum, and several tubes.	.
58. A large example, and cranidia of <i>Elrathia sampsoni</i> .	.

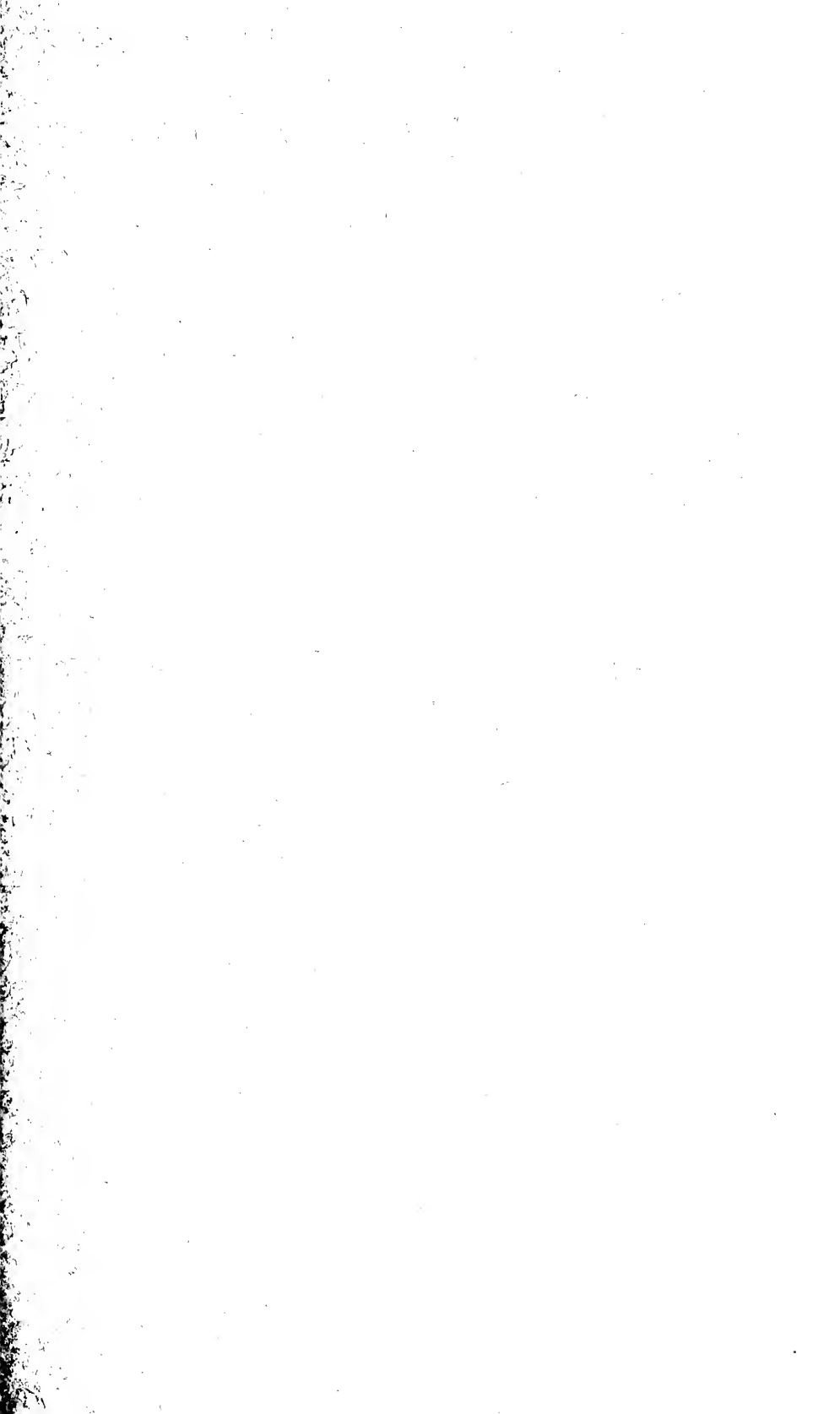
Figs. 1, 2, 12-15, 24-26, 31-35, 56, 58, are from Loc. 37m.

Figs. 3-11, 16-24, 27-30, 36-55, are from Loc. 37n.



MIDDLE CAMBRIAN FOSSILS FROM PEND OREILLE LAKE, IDAHO

(For explanation, see page 11.)





SMITHSONIAN MISCELLANEOUS COLLECTIONS

VOLUME 97 NUMBER 4

THE FEEDING MECHANISM OF ADULT LEPIDOPTERA

BY

JOHN B. SCHMITT

Assistant Entomologist, New Jersey Agricultural
Experiment Station, New Brunswick



(PUBLICATION 3448)

CITY OF WASHINGTON
PUBLISHED BY THE SMITHSONIAN INSTITUTION
JANUARY 10, 1938

SMITHSONIAN MISCELLANEOUS COLLECTIONS
VOLUME 97. NUMBER 4

THE FEEDING MECHANISM OF ADULT LEPIDOPTERA

BY

JOHN B. SCHMITT

Assistant Entomologist, New Jersey Agricultural
Experiment Station, New Brunswick



(PUBLICATION 3448)

CITY OF WASHINGTON
PUBLISHED BY THE SMITHSONIAN INSTITUTION
JANUARY 10, 1938

The Lord Baltimore Press
BALTIMORE, MD., U. S. A.

THE FEEDING MECHANISM OF ADULT LEPIDOPTERA

By JOHN B. SCHMITT

*Assistant Entomologist, New Jersey Agricultural
Experiment Station, New Brunswick*

CONTENTS

	PAGE
Introduction	I
I. General structure of the head and mouthparts.....	2
II. The proboscis	5
Structure and musculature.....	5
Mechanism of coiling and extension.....	8
Comparative structure in lepidopterous families.....	8
III. The sucking pump.....	16
Generalized structure	17
Pump of lepidoptera.....	18
Mechanism	20
Comparative structure in lepidopterous families.....	20
IV. The labium	24
V. Summary	26
Abbreviations used on the figures.....	27
References	28

INTRODUCTION

The mechanism of the feeding apparatus of moths and butterflies has been studied by a number of anatomists since Reamur and Latreille, but the exact means by which the proboscis is extended has not been determined, and it is this problem with which this paper is chiefly concerned. The morphology of the sucking pump has also engaged the writer's attention, as have various other parts of the lepidopterous head.

The literature is not extensive and (as the general information on the head is contained in most textbooks) there is little need except for historical purposes to review the contributions previous to the work of Burgess (1880) who was the first worker to describe correctly the muscles within the proboscis. Kirbach (1883) wrote on the sucking pump of *Vanessa io* and also on the muscles within the proboscis. In 1890 Burgess published further information on the structure of the head of the milkweed butterfly, followed by Kellogg (1893) on the same subject. In 1895 Kellogg showed that the pilifers are labral lobes

and not mandibles. Berlese's "Gli Insetti" (1910) contains some information on the maxillary musculature. Tillyard (1923) demonstrated that the maxillary lobes forming the proboscis are probably the galeae. Weber (1924) has contributed to our knowledge of the occipital area and the cervix of certain species. Snodgrass (1935) described the sucking pump of a sphingid.

This study was made possible only through the invaluable instruction and encouragement of R. E. Snodgrass, of the Bureau of Entomology and Plant Quarantine of the United States Department of Agriculture, and I am therefore especially indebted to him. I am also indebted to Dr. T. J. Headlee, of Rutgers University, and to Dr. E. N. Cory, of the University of Maryland, for their cooperation while at their respective institutions. I also appreciate the aid of Dr. A. B. Klots, of the City College of New York, in determining microlepidoptera. This study formed the larger part of a thesis submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy at Rutgers University.

I. GENERAL STRUCTURE OF THE HEAD AND MOUTHPARTS

The cranium of the lepidopterous head is a relatively simple structure showing very few sutures. The clypeus forms an elongate anterior area and is not marked off from the frons. A suture extends on each side from the invagination of the anterior arm of the tentorium to the antenna fossa in the butterflies and most of the higher moths, but is usually absent in the more generalized groups. Whether this suture is a true frontal suture is questionable, for, as will be seen later, its internal ridge seems to have been developed secondarily for the purpose of bracing the cranium against the pull of the antenna muscles, which originate on the anterior arms of the tentorium. The internal ridge of this suture will be called the antennal ridge (fig. 1, A, *AR*). The parietals are large, and in the higher Lepidoptera their size is further increased by the great development of the compound eyes. The ventral and anterior ends of each parietal are recurved mesally, thereby providing between them a recess for the maxillae and the labium (fig. 12, B). Posteriorly and dorsally, the parietals merge with the occiput, there being no limiting suture. The postoccipital suture has a well-developed internal ridge and is itself usually evident externally. It limits the dorsal part of the posterior edge of the occiput, the ventral part being limited by the much lengthened hypostomal sutures. The invaginations of the posterior arms of the tentorium are located in the ends of the postoccipital suture, and since most of each hypostomal suture lies in the same dorsoventral line as the lateral part

of the postoccipital suture, the posterior tentorial pits appear to be "higher" in the lepidopterous head than they are in most other insects. Internally, this part of the hypostomal suture is marked by a well-developed ridge, on which are inserted the ventral intersegmental muscles from the thorax. The postocciput and the posterior part of the hypostoma are either poorly developed or entirely membranous.

The ventral areas of the parietals are not marked off from the subgenal areas by sutures, so it may be said that the pleurostomal and anterior part of the hypostomal sutures are nonexistent. Since the invaginations of the anterior tentorial arms of pterygote insects are always found in either the pleurostomal or the epistomal sutures, it might be supposed that the furrow extending ventrally from each anterior tentorial pit is the pleurostomal suture. Such, however, is not the case. This deep infolding is the line along which the clypeus and the parietal have been brought into juxtaposition, so that the true pleurostomal suture would necessarily be within the infolded area. In some groups, as in the Tineidae and the Pyralidae, this infolding is not pronounced, but in the butterflies it is extremely well developed. From a practical viewpoint, these infolded ridges are continuous with the ridges that brace the floor of a sucking pump, and will be described later.

The cephalic endoskeleton, or tentorium, of moths and butterflies presents practically the same structure throughout the order (fig. 1 A). The anterior arms of the tentorium are well developed and are the most important part. They are without dorsal arms, and the antennal muscles arise directly on them. The anterior arms are attached to the posterior bridge, close to the invaginations of the posterior arms. In many cases the actual posterior tentorial pits are really large open depressions, so that when seen from the inside of the head the anterior arms and the tentorial bridge appear to have separate invaginations. The posterior bridge is always small and poorly developed, and no muscles actually arise on its span.

The only muscles arising on the anterior arms of the tentorium are the antennal muscles and two pairs of muscles affecting the extension of the proboscis, which will be described later. In the butterflies and in moths having functional mouth parts the tentorial arms are often provided with large flanges and ridges, to allow greater attachment surface. In moths having degenerate or obsolete mouthparts the tentorial arms are often bulging and thin-walled, especially in the anterior halves.

The foramen magnum is sharply constricted near the invaginations of the posterior tentorial arms, although the degree of constriction

varies considerably throughout the order. However, the posterior bridge of the tentorium is always short.

The mouth parts of adult Lepidoptera consist of the maxillae, the labium, the labrum, and the hypopharynx. The maxillae, as is well known, are the most important, their galeae forming the long succtorial proboscis in those which have functional feeding mechanisms. Various degrees of degeneracy may be found, until the point is reached, as in the males of *Thyridopteryx*, where the maxillae are no longer recognizable as distinct appendages. The hypopharynx of moths and butterflies is incorporated in the floor of the sucking pump

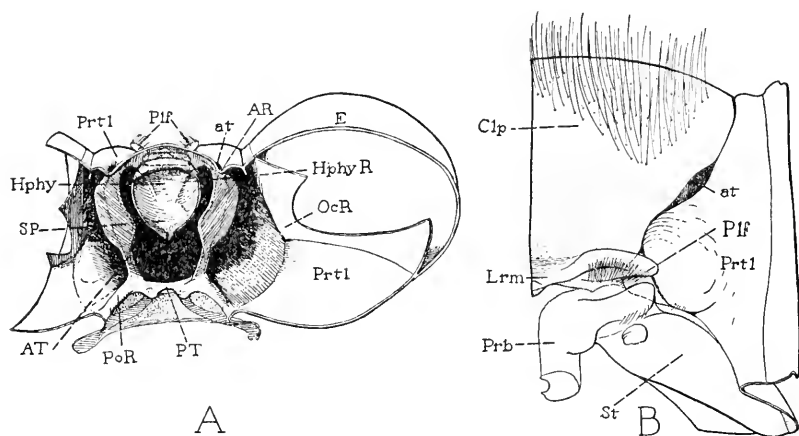


FIG. 1.—Structural details of the head and feeding mechanism of *Argynnis* and *Danaus*.

A, right half of head, mesal view, of *Argynnis cybelle*, showing endoskeleton and floor of sucking pump (SP) formed by hypopharynx (Hphy). B, left half of clypeus and base of left maxilla attached to parietal part of head of *Danaus menippe*, anterior view.

and will be described under that heading. The labrum, like the hypopharynx, is really a part of the cranium, but since it plays a part in the mechanics of feeding it may be described as a mouthpart. The lateral lobes of the labrum, called the *pilifers*, bear against the proboscis base, and in some butterflies the labrum is sufficiently flexible to move as a unit with the proboscis base. In such cases (fig. 1 B) the proboscis base is provided with a knob that fits against the pilifer under its fringe of setae. In many moths, however, the labrum does not have this function. The labium is evident only as a small triangular area bearing the three-segmented labial palpi. These palpi are usually so placed that the coiled proboscis can be clasped between them and be almost completely hidden from view. The labial palpi

are capable of some motion, each palpus having usually one or two muscles at its base, which enable the palpi to clasp the coiled proboscis or to release it.

The mouth cavity, or preoral cavity, is defined by Snodgrass (1935) as "an external space bounded anteriorly by the epipharyngeal wall of the labrum and clypeus, posteriorly by the labium, and laterally by the mandibles and the maxillae." The hypopharynx is described as lying in this cavity as a tonguelike lobe. The cibarium is that part of the preoral cavity which is anterior to the hypopharynx; that is, the anterior surface of the hypopharynx forms its "floor." The salivary meatus is the portion of the preoral cavity which is posterior to the hypopharynx, i. e., enclosed between the hypopharynx and the anterior surface of the prementum. The median salivary duct pours its secretions into this cavity from a small pocket called the salivarium, between the labium and the hypopharynx.

In the Lepidoptera most of the cibarium is incorporated with a part of the pharynx in the sucking pump, as will be demonstrated later. There is a small portion of the epipharyngeal surface which is not a part of the sucking pump, and this part is usually applied against the proboscis base. The salivary meatus is practically nonexistent, as the hypopharynx has completely lost its lobular character, and there is no protrusion of a prementum beyond the salivarium. The hypopharynx, in fact, forms most of the "floor" of the sucking pump (fig. 1 A) as a single well-sclerotized piece.

II. THE PROBOSCIS

Savigny long ago discovered that the proboscis of Lepidoptera is derived from the maxillae or rather from one pair of the lobes of the maxillae. The cardo and the stipes are usually quite distinct, and form no part of the proboscis as such; hence the term *proboscis* should be reserved for the conveying structure itself. Tillyard (1923) has produced evidence that the proboscis is derived from the galeae.

Structure and musculature.—Each half or unit of the proboscis is therefore a tube, the lumen of which is continuous with the body cavity through the stipes. Each proboscis unit is rendered flexible by a series of fine rings separated by membrane, as described by Burgess. These rings are absent in nonfunctional proboscides. In the butterflies and higher moths the rings are made up of many small flat circles of hard cuticula, like small beads set in rows. The food channel is also lined with rings, similar but having only about one-third the width of the outer rings. Muscles passing obliquely between the rings were

described by Burgess as effecting the coiling of the proboscis, a finding verified by Berlese and later writers.

The cardo in functional maxillae is usually a small flat sclerite just anterior to the labial palpi. The stipes varies in shape throughout the

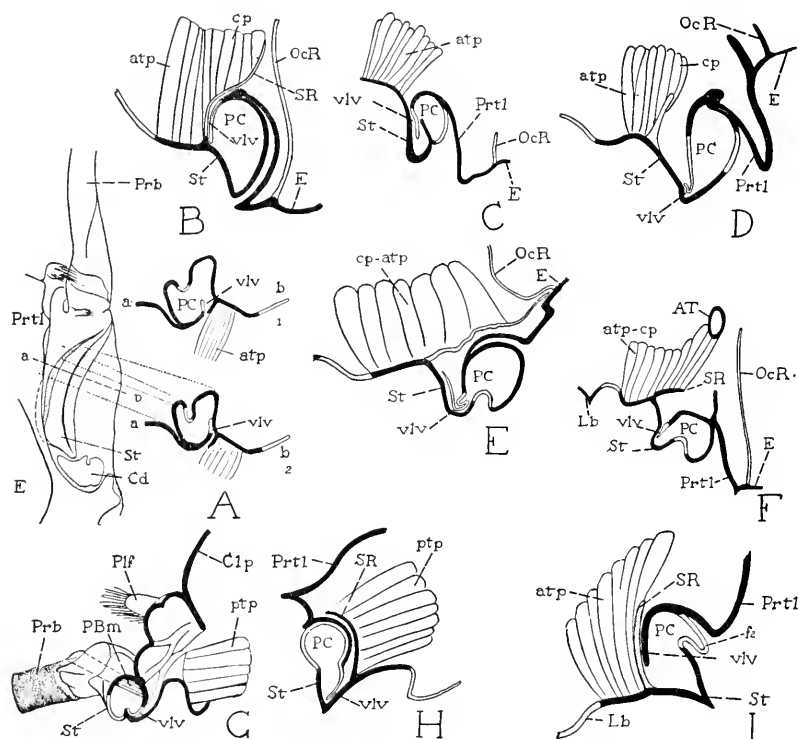


FIG. 2.—Pressure-producing mechanisms of the maxillae.

A, base of right maxilla of a swallowtail butterfly, ventral view (morphologically posterior), showing at *A*, a cross-section through the line *ab*, giving appearance of stipes when proboscis is coiled. B, cross-section of stipes of *Catocala* sp., showing appearance of pressure chamber (PC) formed by stipes. C, same of *Arcyonis alope*. D, same of *Hemaris thysbe*. E, same of *Danaus menippe*. F, same of *Pieris rapae*. G, base of proboscis of *Danaus menippe*, lateral view, showing insertion of posterior tentorial proboscis extensor (*ptp*). H, cross-section of stipes of *Hemaris thysbe* near insertion of posterior tentorial proboscis extensor (*ptp*). I, cross-section of stipes of *Atrytone zabulon*, showing appearance of pressure chamber.

families above the Tineidae, but when functional always presents fundamentally the same structures. The proximal portion in cross-section always has a median flat sclerite continuous with a tubular lateral part (fig. 2). This tubular part fits into the recurved ventral and anterior ends of the parietal, the lateral edge of the stipes being

continuous with the parietal. In some cases the curved lateral part of the proximal portion of the stipes is membranous, as in *Cercyonia alope* (fig. 2 C). In others the lateral part is heavily sclerotized and the tubular half is modified so that in effect there are two tubes set side by side with membrane between. This arrangement is found in the Pieridae (fig. 2 F). The distal portion of the stipes is also recessed under the parietal. The mesal surfaces of the maxillae bear against each other or against a small projection of the labium.

In addition to the muscles within the proboscis mentioned above there are three pairs of maxillary muscles inserting on each stipes and originating within the cranium. Two of these muscles originate

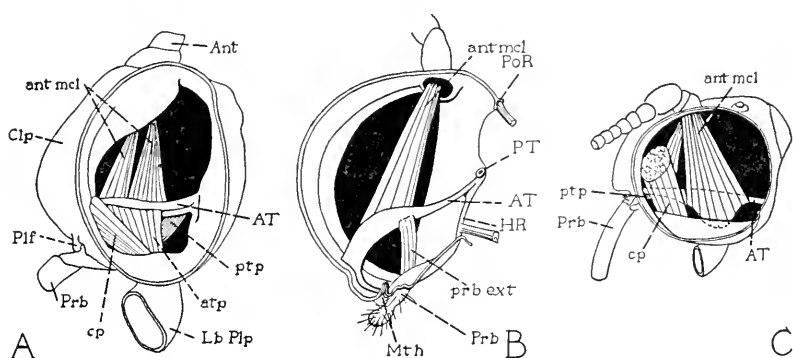


FIG. 3.—Proboscis extensor musculature.

A, left half of head of *Danaus menippe*, showing interior by removal of eye. B, right half of head, mesal view, of *Thyridopteryx ephemeraeformis* (male), as exposed by median sagittal cut. C, left half of head of *Desmia funeralis*, showing interior by removal of eye.

on the anterior arm of the tentorium, and the third originates on the anterior part of the gena. Of the tentorial muscles, one arises on the lateral surface of the anterior arm and inserts on the distal part of the stipes, on the median flat sclerite. It is therefore called the *anterior tentorial proboscis extensor* (fig. 3 A, *atp*). The second muscle originates on the mesal surface of the anterior arm of the tentorium and inserts near the distal point of the stipes. Its origin on the tentorium is always posterior to that of the anterior tentorial proboscis extensor, so that the paths of these muscles cross within the head. This second muscle is called the *posterior tentorial proboscis extensor* (fig. 3 A, *ptp*). The genal muscle originates on the anterior part of the gena and inserts on the flat mesal sclerite of the stipes. It is called the *cranial proboscis extensor* (fig. 3 A, *cp*).

Mechanism of coiling and extension.—It should now be possible to understand the functions of these muscles. A study of figure 2 shows that by their contraction, the anterior tentorial proboscis extensors draw the tubular part of the stipes up against the recurved end of the gena. (This action is shown diagrammatically in fig. 2 A.) It will be noticed that there is a valve arrangement between the tubular part of the stipes and the flat sclerite on which the muscles are inserted. As the muscles draw the stipes upward, the valve (*v/v*) closes, with the result that the tubular part becomes a closed cylinder. Thus pressure is exerted against the blood within the stipes cylinder as it is forced against the recurved flange of the gena. The stipes cylinder forms a closed point at its proximal end, and therefore the blood displaced as the pressure continues must move outward through the stipes, toward the proboscis. The stipital ridge is enlarged at the proximal end of the stipes and thus practically covers the lumen of the proboscis unit. The posterior tentorial proboscis extensor is inserted on this ridge, and contraction of this muscle not only creates pressure on the blood enclosed within the stipes, but also moves the base of the proboscis unit upward, which effects a tight seal with the functional mouth (fig. 2 G, H; 9 D).

The blood displaced from the stipes is thus forced out into the lumen of each tightly coiled proboscis unit, thereby causing the proboscis to unroll. The diagonal muscles within each proboscis unit, described by Burgess, cause the proboscis to coil. That blood pressure might be the agency for uncoiling the proboscis was first suggested to the writer by R. E. Snodgrass, who, in his "Principles of Insect Morphology" points out the mechanical analogy of such a mechanism with the toy paper snake which a child uncoils by blowing into it. The uncoiling action of one proboscis unit is shown diagrammatically in figure 4.

The mechanism described above is the simplest which the writer has seen. In many moths and butterflies the stipital cylinder is further modified, but the principle is invariably the same, as may be seen in figure 2. The musculature concerned in the extension of the proboscis seems to be fundamentally the three pairs of muscles described, but in a large number of insects one or two pairs may be absent. However, functional maxillae always have at least two pairs.

Comparative structure in lepidopterous families.—The maxillae of a number of species representing the more important families were examined, primarily to determine the fundamental musculature of the lepidopterous maxilla. Moths having degenerate or obsolete mouthparts were also studied and, indeed, proved to be one of the most interesting phases of this investigation. To expose the proboscis extensor musculature, a simple procedure is first to make a complete

median sagittal cut, and then, using either half of the head, to remove the compound eye, the brain, subesophageal ganglion, and the sucking pump.

Tineidae: In the females of the common Yucca moth, *Pronuba yuccasella*, all three pairs of proboscis extensors are present, very much as described above. There is a single muscle at the base of each maxillary palpus and each maxillary tentacle. The common clothes moth, *Tineola*, lacks the cranial proboscis extensors, but otherwise its musculature is complete. In certain other *Tineidae*, determined

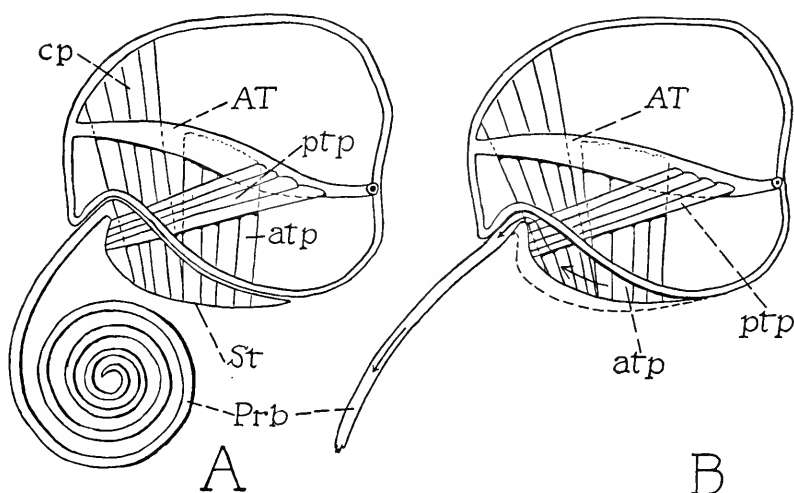


FIG. 4.—Diagram of the action of the proboscis extensor muscles of the right half of the head, mesal view.

A, proboscis coiled. B, proboscis extended by blood forced into it by compression of stipes (see fig. 2).

to family only, there are no tentorial muscles but only the cranial proboscis extensors, a very unusual condition.

Coleophoridae: A number of coleophorids, determined to family only, were found to possess both pairs of tentorial proboscis extensors, but to lack the cranial proboscis extensors.

Limacodidae: A single representative, *Euclea cloris indeterminia*, was studied. This moth has practically no proboscis, but only two very small lobes, each a remnant of a proboscis unit. A single pair of tentorial proboscis extensors is all that is left of the maxillary musculature.

Oecophoridae: A species of the genus *Agonopterix*, with a well-developed proboscis, was also examined. All three pairs of extensors

are well developed, and strands of the anterior proboscis extensor have migrated onto the clypeus, so that there appears to be a fourth pair of muscles.

Pyalidae: In the pyralids examined, the cranial proboscis extensor is often absent. In the common wax moth, *Galleria mellonella*, both tentorial muscles are clearly evident and apparently able to act. The proboscis does not appear to be functional, and it is probable that the proboscis extensors serve only to move the maxillary palpi. The lesser wax moth, *Achroia grisella* Fab., has only remnants of the tentorial extensors, the proboscis being evident only as two short lobes, apparently nonfunctional. Two other pyralids, *Nomophila noctuella* and *Ephestia kuehniella*, have the proboscis well developed. The musculature is complete and the cranial muscle is especially well developed.

In figure 3 C the head of a pyralid, *Desmia funeralis*, is represented with the left eye removed. In this case all three proboscis extensor muscles are present, although the anterior tentorial proboscis extensor is very small. The cranial proboscis extensor is remarkably large, but since it originates on the ocular ridge, a relatively thin structure, it may be doubted whether it exerts much force. It may also be seen that a large lobe has been formed on each anterior tentorial arm in order to accommodate a very large antennal muscle, thereby depriving the proboscis extensor muscles of their usual position. Such a sacrifice of feeding structures for nonfeeding structures may be found in many moths.

Tortricidae: The tortricids usually possess all three pairs of proboscis extensors. Figure 10 B represents the head of the common codling moth, *Carpocapsa pomonella*, as seen when opened by a median sagittal cut. The sucking pump is shown in place, but the tentorial extensors may be seen just below the pump.

Psychidae: The male of the common bag-worm moth, *Thyridopteryx ephemeraeformis*, was studied in this group. These moths were found to have an extremely degenerate proboscis (fig. 3 B) represented only by two large lobes. Each lobe has a single proboscis extensor muscle, arising on the anterior arm. The antennal muscles, however, are by far the largest muscles in the head.

Sphingidae: The feeding mechanisms found in this family are generally very well developed. The musculature of the head of one species of sphingid, *Sphinx convolvuli*, has already been described to some extent by Berlese (1910). The proboscis musculature which he found homologizes thus: his no. 190 is the cranial proboscis extensor, his no. 171 is the anterior tentorial proboscis extensor, and his no. 172 is the

posterior tentorial proboscis extensor. However, Berlese apparently did not examine the insertions of these muscles and makes no reference to their functions. In discussing the possible mode of extension of the proboscis Berlese followed the suggestion of Burgess, that it is unrolled by its own elasticity.

The proboscis musculature of one species of sphinx moth, *Hemaris thysbe*, may be taken as generally typical of the family. In this moth (fig. 10 D) the tentorial muscles are equally well developed and are well spaced on the anterior arms of the tentorium. The cranial proboscis extensor is moderately developed and in general the whole arrangement is well balanced.

Yet, in some sphingids, there are decidedly inferior proboscis extension mechanisms. For example, the sucking pump in *Smerinthus geminatus* is so large that there is very little space left for the proboscis musculature, and the brain also is reduced in size and displaced posteriorly (fig. 10 C). In this moth there is no cranial proboscis extensor, and only one tentorial muscle, which appears to be the posterior tentorial proboscis extensor judging by its insertion. Another sphingid, *Darapsa pholus* (fig. 6 B), has an extremely large cranial proboscis extensor.

Geometridae: The feeding mechanisms of members of this family are weak or degenerate. The proboscis musculature of *Haematopsis grataria* is shown in fig. 9 C. All three stipital muscles are present, but very weak, especially the tentorial muscles. The cranial proboscis extensor is also very short. In the little green geometrids (subfamily Hemitheinae) the proboscis musculature resembles that of *Haematopsis*.

The geometrid *Ennomos subsignarius* is typical of further degeneracy in this family. Only the tentorial muscles are present and they are very weak (fig. 5 B). Each anterior arm is very thin-walled and is considerably enlarged. This enlargement, of course, "lightens" the head by replacing blood volume with air and is of interest in view of the remarkable flights of this insect. *Caberodes confusaria* resembles *Ennomos* in this respect but has a functional cranial proboscis extensor.

The adults of the spring cankerworm, *Paleacrita vernata*, differ, as is well known, in that the males are winged and the females wingless. However, there is practically no difference between the sexes in the proboscis and its musculature. The proboscis itself, in both cases, is represented by two small lobes. Only a pair of tentorial proboscis extensors can be found, and they are very weak.

Noctuidae: In this family the proboscis and its musculature are very well developed. The cranial proboscis extensor here reaches a remarkable size and importance, in comparison with the tentorial proboscis muscles. This is of interest in view of the fact that the cranial proboscis extensor is the muscle most frequently absent in cases where there is not a full complement of proboscis muscles. The proboscis musculature of a large moth, *Catocala nubilis*, is shown in figure 6 A and is in general typical of the family.

Arctiidae: All examined members of this family have degenerate feeding mechanisms. Figure 6 C shows a section through the head of a typical species, *Apantesis virgo*. Both *A. virgo* and *A. vittata* have

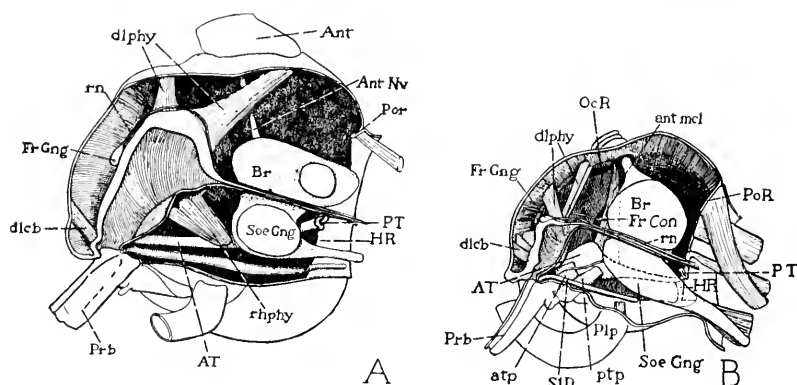


FIG. 5.—Proboscis extensor musculature and the sucking pump.

A, right half of head, mesal view, of *Hecmatopsis grataria*, as exposed by median sagittal cut. B, same of *Ennomos subsignarius*.

all three pairs of proboscis extensors. The posterior tentorial proboscis extensor originates well back on the anterior arm of the tentorium. *Estigmene acraea* and *Utetheisa bella* show about the same conditions.

The members of the genus *Haploa* exhibit the strongest proboscis musculature seen in this family, and there can be but little doubt that the proboscis is functional. The members of the genus *Diacrisia*, on the other hand, have the most degenerate feeding mechanisms seen in this family. In *D. virginica* the anterior tentorial proboscis extensor has been lost and the posterior muscle is very weak. The cranial proboscis extensor is still evident.

In *Isia isabella* all three pairs of proboscis muscles are present and apparently functional. The anterior tentorial proboscis extensor, however, has migrated to the antennal ridge, above the anterior arm.

Saturnoidea: The degeneracy of the feeding mechanism in the giant silk moths is so complete that there are few traces left of the

proboscis musculature. In the large moth *Samia cecropia*, for example, the proboscis is represented by two small shapeless lobes (fig. 11 B, *Prb*), associated with which there is a single pair of tentorial muscles. The position of these muscles suggests that they may be the posterior tentorial proboscis extensors.

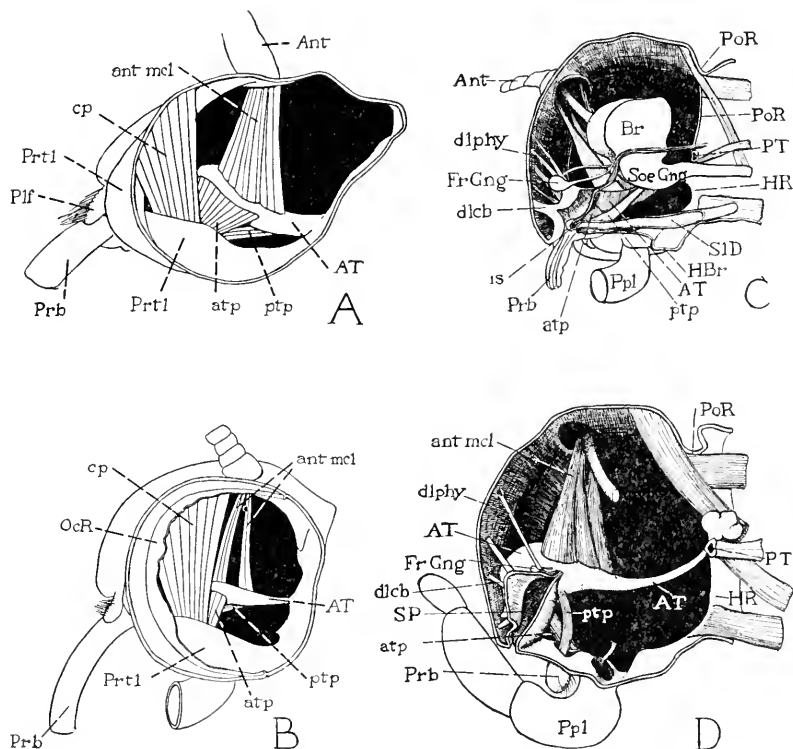


FIG. 6.—Proboscis extensor musculature.

A, left half of head of *Catocala nubilis*, showing interior by removal of eye. B, same of *Darapsa pholus*. C, right half of head, mesal view, *Apantesis virga*, as exposed by median sagittal cut. D, same of *Malacosoma americana*.

The tentorium of this moth has developed a peculiar secondary function. In addition to having the anterior part of the anterior arms thin-walled and bulging, displacing blood with air, the posterior part of the anterior arms is tubular and curved to provide a sort of cradle for the brain and suboesophageal ganglion. This is done by having each arm pass between the brain and the optic lobe on its side. If it were not for this the brain would be supported only by the optic lobes.

In other saturniids remnants of one or both pairs of the tentorial proboscis muscles can be found, but the cranial proboscis extensor is

invariably absent. In *Basilona imperialis* (Ceratocampidae) the proboscis still has a tubular shape and shows a food channel. Both tentorial muscles are present, but no cranial muscle.

In all saturniids examined, the position of the tentorium in the head—that is, the length of the hypostomal area below the posterior tentorial pits—suggests that the ancestors of these moths had powerful feeding mechanisms with the tentorial muscles well developed. The antennal muscles in these moths are always large and powerful, and it may be that the great enlargement of the anterior part of the anterior arms results from the need for a large base for these muscles rather than from an effort to lighten the head. However, the latter purpose is unmistakably served.

Lasiocampidae: The adult of the eastern tent caterpillar, *Mala-cosoma americana*, was studied as an example of a lasiocampid, but its resemblance to a saturniid was so complete that no new information was obtained. The antennal, proboscis, and sucking pump musculature is illustrated in figure 6 D.

Bombycidae: Similar conditions were found in the common silk moth, *Bombyx mori* (fig. 7 A). The proboscis is represented by two shapeless lobes. Both pairs of tentorial muscles are present.

Papilionoidea: Representatives of five families of butterflies were studied, and some interesting differences were found. In the Nymphalidae and Danaidae the three pairs of proboscis extensors are most perfectly preserved. Figure 11 shows the proboscis extensor of *Danaus menippe*, known as the "Monarch butterfly." All three pairs of muscles are well developed. The musculature of *Vanessa atalanta*, the red admiral butterfly, closely resembles it, as does also the mourning cloak butterfly, *Aglais antiopia*, and the great spangled fritillary, *Argynnis cybele*. In certain other Nymphalidae, however, the cranial proboscis extensor has been lost. Such butterflies include the viceroy, *Basilarchia archippus*, and the common grayling, *Cercyonis alope*. A few species of Lycaenidae were also examined. In *Lycaenopsis argiolus*, the common blue, and *Everes comyntas*, the tailed blue, the musculature consists of the familiar three pairs. In *Chrysophanus hypophleas* the cranial muscle has been lost, but both tentorial muscles are well developed.

Thus, in these two families nothing unusual was found. In the Papilionidae and the Pieridae, however, no trace was found of the cranial proboscis extensor, but instead there was a remarkable migration of part of the anterior tentorial proboscis extensor. Inserting on each stipes with the anterior tentorial proboscis extensor but arising on the *clypeus*, between the anterior tentorial arms, there is a single

large muscle. This is illustrated in figure 7 B, showing the musculature of *Pieris rapae*. The migrant is marked atp_2 , and it really passes laterad of the posterior tentorial proboscis extensor, its strands inserting with those of the anterior tentorial proboscis extensor which originate on the anterior arm. *Papilio polyxenes*, *P. troilus*, and *P. marcellus* show similar conditions. Sometimes there is a continuous band of muscle from the clypeus to the anterior arm of the tentorium.

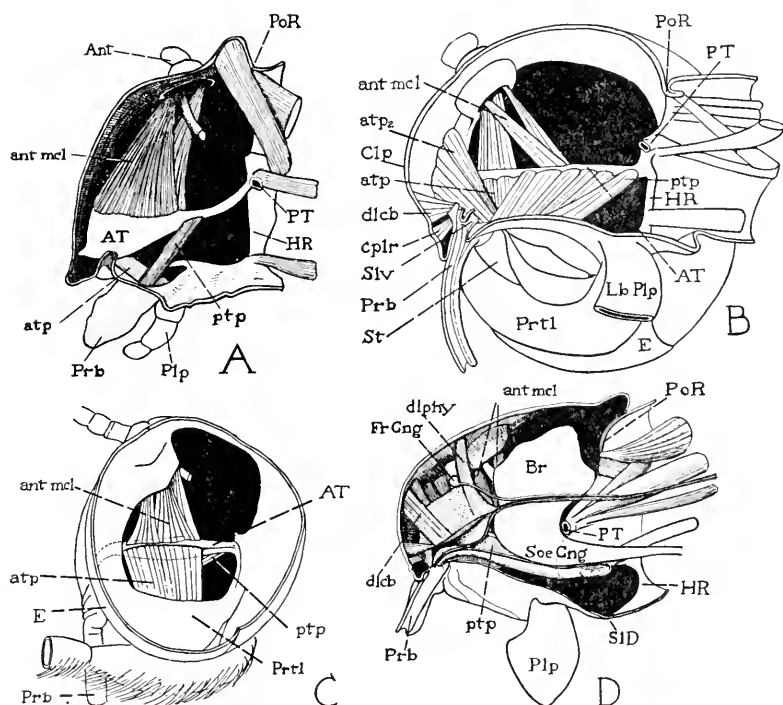


FIG. 7.—Proboscis extensor musculature.

A, right half of head, mesal view, of *Bombyx mori*, as exposed by median sagittal cut. B, same of *Pieris rapae*. C, left half of head of *Pieris rapae*, showing interior by removal of eye. D, right half of head, mesal view, of *Epargyreus tityrus*, as exposed by median sagittal cut.

In the Pieridae this modification is more complete, with the "migrant" atp_2 originating higher on the clypeus than in the Papilionidae. In *Pieris protodice*, the checkered white, this muscle originates just anterior of the antennal socket. The musculature of *Pieris rapae* is illustrated in figure 7 B. Other pierids examined included *Colias eurytheme* and *Anthocharis genutia*.

By eliminating the cranial proboscis extensor, the Papilionidae and Pieridae seem to have considerably narrowed the parietal area, or per-

haps it should be said, increased the extent of the compound eye, yet without sacrificing muscular power. In effect, this muscle is here located between the anterior arm of the tentorium and the anterolateral surface of the sucking pump, thus utilizing what might be characterized as "waste space." At the same time, the development of this muscle is necessarily limited by the sucking pump and its muscles.

A fourth pair of muscles should now be described. This pair consists of one muscle located in each proboscis unit, arising on the stipital ridge and inserting in the proboscis base, and called the *proboscis base muscle* (*PBm*). In direction it is a continuation of the posterior tentorial proboscis extensor. Its position in the head of *Papilio* is indicated in figure 9 B, *PBm*, also in figure 2 G.

Hesperiidae: Only two species of skippers have been examined: *Epargyreus tityrus* and *Atrytone zabulon*. In this family the proboscis extensors are short but very well developed. The anterior arms are greatly broadened to provide greater attachment surface, while the cranial proboscis extensors in *Epargyreus* have invaded the antennal ridge to secure greater attachment surface.

The remarkable simplicity of the stipital tube in *Atrytone* is well worthy of note. In figure 2 I it is represented in cross-section under compression. In this type, closure of the pressure chamber is effected directly by the cranial proboscis extensor, as it presses the membranous stipital ridge against the recurved flange of the parietal. The membranous fold labeled *F2* becomes much larger as it approaches the base of the proboscis unit, at which point its outer portion is firmly sclerotized, while its inner lateral section (that is, its morphologically lateral section) remains membranous.

III. THE SUCKING PUMP

Among the orders of insects equipped with sucking pumps, the Hemiptera and the Diptera have received considerable study. Snodgrass (1935) has shown that the pump of the cicada is prepharyngeal in origin and evolved almost entirely from the preoral cibarium. Similarly, Jobling (1929) and Snodgrass (1935) have demonstrated that the sucking pump in Diptera is derived from the cibarium. In respect to the sucking pump of the Hymenoptera, Snodgrass (1935) states that "while the morphology of the organ is not entirely clear, . . . judging from the musculature, it includes without doubt the pharynx and the buccal cavity and perhaps the cibarium." It is, therefore, of interest to determine to what extent the sucking pump of Lepidoptera is preoral in derivation.

Generalized structure.—In the more generalized insects there is usually a large preoral cavity bounded anteriorly by the epipharyngeal wall of the labrum and clypeus, laterally by the mandibles and the maxillae, and posteriorly by the labium. The hypopharynx is suspended between these organs (fig. 8 A, *Prc*) and thus divides the preoral cavity into an anterior *food meatus* (*fm*), having the anterior wall of the hypopharynx for its floor, and a posterior *salivary meatus* (*sm*) enclosed between the posterior wall of the hypopharynx and the anterior surface of the prementum.

The food meatus, of course, is not part of the stomodaeum, but simply space enclosed by certain mouthparts. It leads to the true mouth which marks the beginning of the alimentary canal. A portion

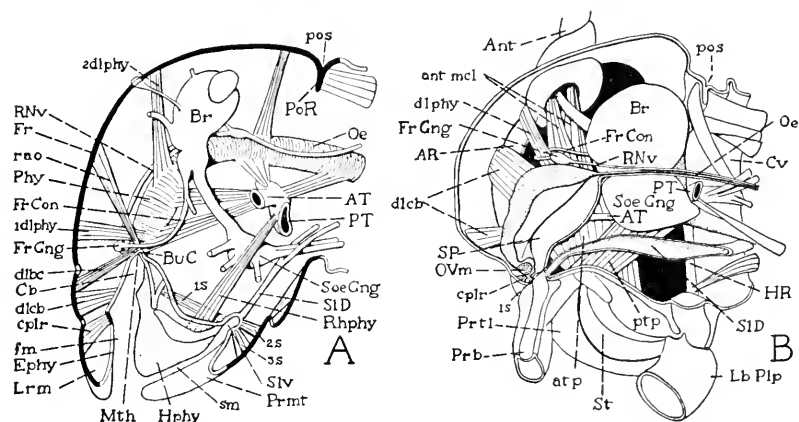


FIG. 8.—Comparison of the orthopteroid head with the lepidopterous head.

A, diagram of orthopteroid head (from Snodgrass). B, right half of head, mesal view, of *Danaus menippe*, as exposed by median sagittal cut.

of the food meatus just before the mouth is used to hold food before swallowing and is therefore known as the *cibarium* (fig. 8 A, *Cb*). The dilators of the cibarium always arise on the clypeus.

The part of the stomodaeum just inside the mouth is termed the *buccal cavity* (*BuC*). Beyond the buccal cavity, extending to the cerebral nerve connectives, we may distinguish the *pharynx* (*Phy*). The dilators of the buccal cavity (*dlbc*) arise on the clypeus, but the dilators of the pharynx (*dlphy*) arise on the frons. The frontal ganglion (*Fr Gng*) lies on the anterior wall of the stomodaeum between the buccal cavity and the pharynx. The connectives of the frontal ganglion (*Fr Con*) always pass laterad of the dilators of the pharynx. From figure 8 A it may be seen that the pharyngeal dilators are thus encircled by two nerve rings, outside of which they cannot migrate.

Pump of Lepidoptera.—Snodgrass (1935) has shown that the sucking pump of moths and butterflies includes at least the buccopharyngeal region of the stomodaeum. This is evidenced by the fact that the dilator muscles of the pump are inserted both before and behind the connectives of the frontal ganglion, which lies on the dorsal wall of the pump. The sucking pump of a butterfly, *Danaus menippe*, is illustrated in figure 8 B showing the dilators of the true pharynx inserted on the posterior portion of the pump. Whether the cibarium or any portion of the food meatus is also incorporated in the lepidopterous sucking pump has therefore been an open question.

The labrum (*Lr*) of moths and butterflies is usually described as a narrow transverse band at the lower edge of the clypeal region, bearing the pilifers (*Plf*) on its lateral extremities (fig. 1 B). In orthopteroid insects there is a pair of muscles, the compressors of the labrum (*cplr*), originating on the anterior wall of the labrum and inserting on the epipharyngeal wall. If the small lobe between the pilifers is the labrum, as it appears to be, this pair of muscles exists in the Lepidoptera (fig. 8 B and 9 B), and the cibarium then necessarily forms part of the anterior section of the pump.

However, there is certain other evidence that the cibarium is included in the pump, based on the structure of the floor of the pump. At the base of the salivary meatus in many generalized insects there is a small cuplike depression or pocket into which the median salivary duct pours its secretions. This pocket is known as the *salivarium* (fig. 8 A, *Slv*). It is supplied with three pairs of muscles, a dorsal pair (*ls*) arising on the suspensorial sclerites of the hypopharynx, and two ventral pairs, arising on the prementum. In the Lepidoptera, only the dorsal pair of muscles, arising on the hypopharynx, may be found. Their point of origin is on the floor of the sucking pump (fig. 9 A, B) showing that the anterior part of the floor is derived from the hypopharynx and therefore that this portion of the sucking pump belongs to the cibarium.

In orthopteroid insects the hypopharynx has a pair of retractors (fig. 8 A, *rhph*) originating on the tentorium. In a geometrid moth, *Haematopis grataria* (fig. 5 A), a pair of muscles was found inserting on the floor of the pump and originating on the anterior arms of the tentorium. Since the ventral dilators of the true pharynx in orthopteroid insects pass *between* the circumoesophageal connectives, they could not possibly migrate from the tentorial bridge to the anterior arms. Hence, this pair of muscles in *Haematopis* must represent the retractors of the hypopharynx, and although they may have migrated beyond the limits of hypopharynx, their presence, neverthe-

less, is evidence that the hypopharynx is incorporated in the sucking pump. In an oecophorid, *Agonopterix* sp., a similar pair of retractors occurs.

The highest development of the sucking pump is to be found in the Sphingidae, the Noctuidae, and especially in the butterflies. Dilation of the pump is produced by the muscles originating on the wall of the head; contraction in the lower moths is produced by the intrinsic elasticity of the pump itself, but in the above-named groups, bands of

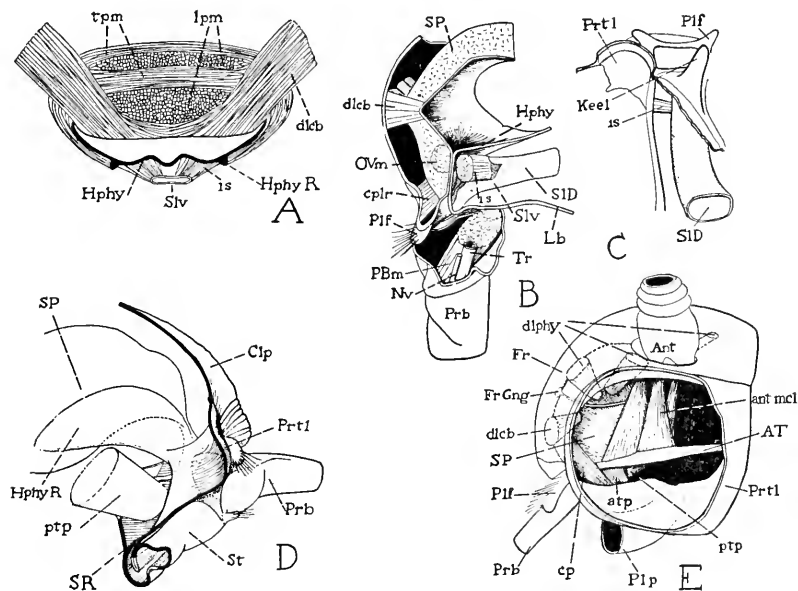


FIG. 9.—Various structural details of the head.

A, cross-section of sucking pump of *Danaus menippe*. B, mesal view of right half of head and base of right proboscis unit of *Papilio* sp. C, ventral view of salivarium of *Lycacnopsis argiolus*. D, base of proboscis and sucking pump of *Papilio* sp. as seen from right side. E, left half of head of *Haematopsis grataria*, showing interior by removal of eye.

muscles passing around the pump are mainly responsible. The "floor" of the pump is heavily sclerotized and well braced to withstand the pull of the dilating muscles. Figure 1 shows the pump in a specimen cleared in KOH, with a portion of the dorsal wall of the pump removed. The infolded ridge on each side between the parietal and the clypeus can be seen passing under the floor of the pump (*HphyR*), thus providing support. Morphologically, these ridges are more difficult to trace. Figure 9 D shows the bracing arrangement of the pump of a butterfly, *Papilio* sp. The infolded ridge between the clypeus

and the parietal can be seen to merge with the hypopharyngeal ridge, which is apparently formed jointly by the epipharynx and the hypopharynx. In effect, the hypopharynx has contributed the median surfaces of each ridge and the area in the floor of the pump between the ridges. The dorsal dilators (*1s*) of the salivarium usually arise on these ridges, indicating that at least that much is hypopharynx.

The dorsal wall of the pump varies greatly throughout the order in the particular arrangement of its dilating muscles, but shows interesting consistency in the relative development of the true dilators of the pharynx and the dilators of the cibarium. Moths beginning with the Tineidae were examined, but no means was found whereby muscles which might be dilators of the buccal cavity could be differentiated from dilators of the cibarium. Therefore, any dilator muscles not included in the frontal complex (i. e., encircled by the connectives of the frontal ganglion, hence true pharyngeal dilators) are labeled as dilators of the cibarium. With very few exceptions, the true pharyngeal dilators are restricted to the posterior part of the sucking pump. It does not follow, of course, that the portion of the pump derived from the pharynx is necessarily limited to this area; it merely shows the extent to which the dilators of each part have contributed to the musculature of the pump.

Mechanism.—In figure 12 A the complete musculature of the pump of *Danaus menippe* is indicated. The muscles compressing the pump are shown in cross-section in figure 9 A also. These muscles are arranged in two groups, transverse pump muscles (*tpm*) and longitudinal pump muscles (*lpn*), with two layers in each group. Figure 9 A was drawn from a hand-cut section of the pump imbedded in paraffin. Focusing through the section showed that fibers of the transverse pump muscles passed directly into the dilating muscles, indicating a possible origin of the compressor muscles from the dilators.

At the anterior end of the pump, a group of transverse pump muscles are often arranged in a distinct group, forming what Burgess (1880) called the "oral valve" (fig. 8 B, *OVm*). Its purpose is believed to be to prevent the imbibed juices from escaping when the pump is emptied. This arrangement was found to be especially well developed in the butterflies and in the Sphingidae.

Comparative structure in lepidopterous families.—A number of undetermined tineids were examined, including the common clothes moth, *Tincola biselliella*. In this family the axis of the sucking pump, that is, a straight line from the anterior to the posterior end of the pump, is practically perpendicular to the longitudinal body axis. Such a pump is illustrated in figure 10 A. A single pair of pharyngeal

dilators is encircled by the frontal connectives. The remainder of the pump dilators form four or more pairs of well-developed short muscles. The pump musculature of the *Yucca* moth is poorly developed although the pump floor is fairly well sclerotized.

In a coleophorid (fig. 10 A) practically the same type of pump was observed, except that the dilators of the cibarium were grouped an-

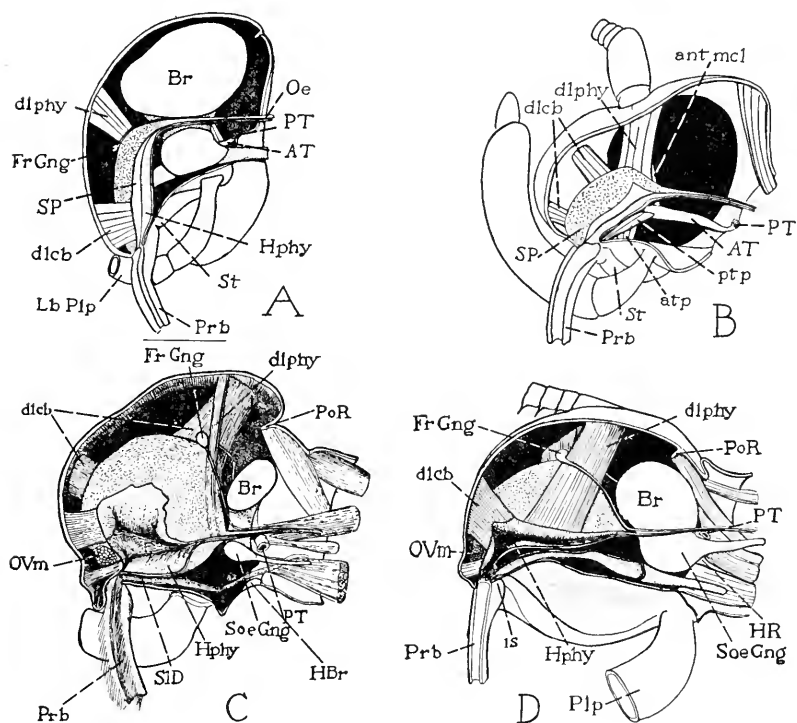


FIG. 10.—The sucking pump.

A, right half of head, mesal view, of *Colcophora coruscipennella*, as exposed by median sagittal cut. B, same of *Carpocapsa pomonella*. C, same of *Smerinthus geminatus*. D, same of *Hemaris thysbe*.

teriorly into a large median band of muscles, with a large band placed laterally on the pump. An oecophorid, *Agonopterix* sp., has a similar and well-developed pump. Males of the common bagworm moth, *Thyridopteryx ephemeraeformis*, possess a very degenerate pump, with the muscles evident but very weak.

In the Tortricidae the axis of the sucking pump is inclined to a more horizontal position. In the codling moth, *Carpocapsa pomonella* (fig. 10 B), there is a single large pair of pharyngeal dilators, and the dorsal

pump wall itself is well supplied with muscles. *Archips* offers nothing unusual in either pump or proboscis.

Excellent development of the sucking pump may be found in such pyralids as *Desmia funeralis* and *Nomophila noctuella*. The cibarial dilators are strong and well spaced, although the pharyngeal dilators are limited to a single pair. In other pyralids, such as the common wax moth, *Galleria mellonella*, and the lesser wax moth, *Achroia grisella*, the pump is relatively weak, especially in the last-named species. Other species of pyralids were studied, but nothing unusual was found.

Sphingidae: Snodgrass (1935) has described the sucking pump of a *Sphinx* moth. In *Hemaris thysbe* the structure of the pump is typical of this family (fig. 10 D). The pair of pharyngeal dilators is large and set close together, and with the cibarial dilators, provide the pump with powerful suction. In one species, *Smerinthus geminatus* (fig. 10 C), this development of the sucking pump has reached such a point that little space is left for the brain and the suboesophageal ganglion. The proboscis extensor musculature is also reduced to a single pair of extensors. In fact, the anterior arms of the tentorium are curved laterally in order to accommodate the expanded pump. In *Darapsa pholus* the pump is of more moderate proportions, although quite well developed. In this species there are two pairs of pharyngeal dilators. A mouth valve or oral valve is common in this family. The dorsal muscles of the salivarium are also easily found in the sphingidae.

Geometridae: In this family the sucking pump is generally weak. Figure 5 B shows the head of a typical geometrid, *Ennomos subsignarius*. There are three pairs of pharyngeal dilators and three pairs of cibarial dilators, but all are relatively thin muscles. The dorsal salivarium muscles are also evident, although very small. *Caberodes confusaris* shows about the same pump as *Ennomos*. The sucking pump of both the males and the females of the spring cankerworm moth, *Palcacrita vernata*, is very weak, although provided with four pairs of dilators.

The sucking pump of *Haematopis grataria*, in addition to possessing a pair of hypopharyngeal retractors (fig. 5 A; *rhphy*), is of interest because of its unusual formation. There are three pairs of pharyngeal dilators, the posterior pair originating posterior to the antennae and passing between the antennal nerves (fig. 9 E). There are also two pairs of cibarial dilators.

Noctuidae: Members of this family possess well-developed sucking pumps, of which that of *Heliothis obsoleta* (fig. 11 A) is typical. Laterally, the pump is provided with a sheet of fibers on each side, the

posterior bundle of which is shown by the position of the frontal connective to be derived from the pharyngeal dilators. In addition to these sheets of muscle, there are two pairs of dilators on the anterior part of the pump. The dorsal salivarium muscles are well developed. The sucking pump of *Autographa falcifera* resembles that of *Heliothis*.

Arctiidae: Moths of this family are provided with poorly-developed feeding mechanisms. Figure 6 C illustrates the head of an arctiid, *Apantesis virgo*. The pump muscles are mere strands, and the floor of the pump is but weakly sclerotized. In *Isia isabella* the pump and

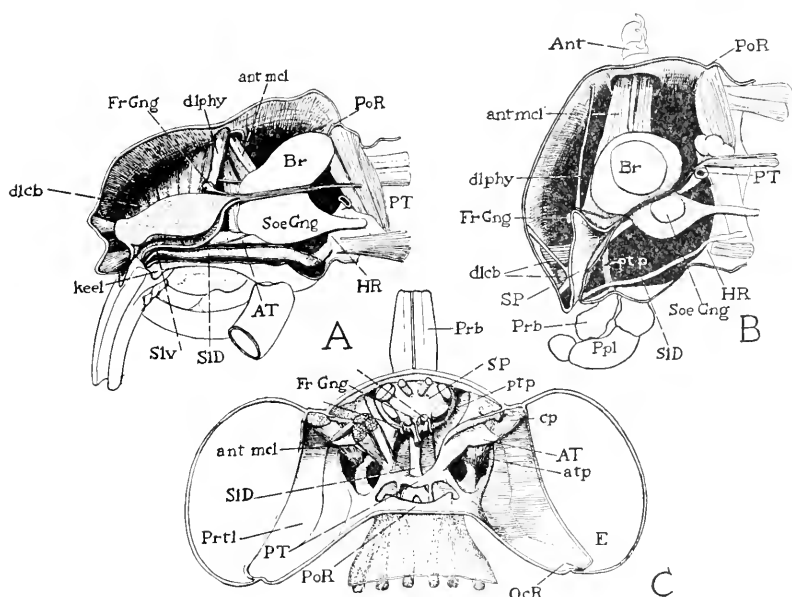


FIG. 11.—The sucking pump.

A, right half of head, mesal view, of *Heliothis obsoleta*, as exposed by median sagittal cut. B, same of *Samia cecropia*. C, head of *Epargyreus tityrus*, as seen with dorsal wall removed.

proboscis are weak but apparently functional. In the genus *Haploa* the pump is relatively strong. *Diacrisia virginica* shows the most degenerate condition observed in this family, the pump dilators being mere strands. Yet, in many arctiids the dorsal salivarium muscles are present and probably functional.

Saturniidae: In this family the sucking pump is extremely weak. Figure 11 B illustrates the sucking pump of *Samia cecropia*. There is a single pair of pharyngeal dilators, still recognizable by means of the frontal ganglion. Laterally, there are two pairs of muscles which might be functional. No salivarium muscles could be found. The

sucking pumps of other saturniids have about the same development as in *Samia*.

Bombycidae: The well-known silk-moth, *Bombyx mori*, also has a very feeble sucking pump (fig. 7 A). The remnants of only two pairs of muscles are present, one pair being pharyngeal dilators.

Ceratocampidae: The sucking pump of *Basilona imperialis* is very weak and in general much as in the saturniids. There are two pairs of pharyngeal dilators.

Lasiocampidae: The adult of the eastern tent caterpillar, *Malacosoma americana*, was studied as an example of this family (fig. 6 D). The pump has a single pair of pharyngeal dilators and three pairs of cibarial dilators, but all are mere threads.

Hesperiidae: The skippers have well-developed sucking pumps, not unlike those of the butterflies. The head of *Epargyreus tityrus* is illustrated in figures 11 C and 7 D. There is only a single pair of pharyngeal dilators, most of the contraction being provided by the anterior muscles.

Papilionoidea: The swallowtail butterflies have a large sheet of muscle on each side of the pump, as well as a pair of median muscles and a pair of pharyngeal dilators. In the family *Pieridae* the pump very much resembles that in *Papilionidae*, except that two pairs of pharyngeal dilators are usually present. The *Nymphalidae* and *Danaidae* show one or two pairs of pharyngeal dilators; in *Argynnis cybele* the dilators of the pharynx originate as two pairs but insert practically as one. The sucking pump of *Danaus menippe* is illustrated in figures 8 B and 12 A.

However, throughout the families of the *Lepidoptera* it is probable that these pairs of pharyngeal dilators do not represent original pairs of muscles immediately homologous with the dilators of the pharynx of such insects as *Dissosteira*. For example, in *Dissosteira* there is a pair of *retractors of the mouth angles* encircled by the frontal connectives, but it is improbable that any of the muscles encircled by the frontal connectives in *Haematopsis* are exactly homologous with the retractors of the mouth angles (see fig. 8 A, *rao*).

IV. THE LABIUM

The structure and limits of the labium in adult *Lepidoptera* have been previously described by other writers, most recently by Snodgrass (1935). In figure 12 B the labium of *Hemaris thysbe* is illustrated. In this case the labium is limited to a median strip passing to the base of the proboscis, and a small area around each labial palpus. Posteriorly, the labium is supported by a hypostomal bridge (*HBr.*).

In the yucca moth, *Pronuba yuccasella*, there is a small paired fleshy lobe at the distal end of the labium. The Oriental fruit moth, *Grapholitha molesta*, also has a pair of minute lobes at the tip of the labium, but it is improbable that these lobes have any significance.

The labium of many moths and butterflies possesses a strong ventral ridge at the distal end (figs. 11 A and 9 C, *Kcel*). A possible function of this ridge is to serve as a bearing surface for the proboscis base.

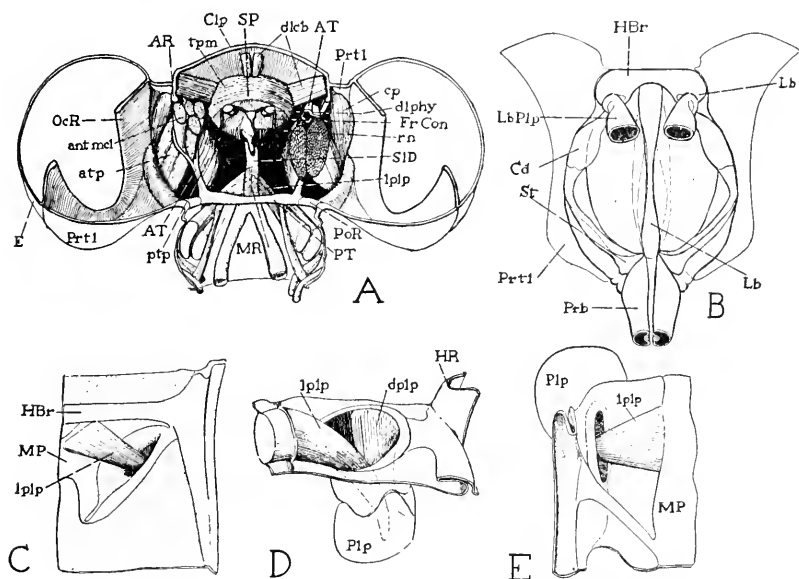


FIG. 12.—Various structural details of the head.

A, head of *Danaus menippe*, as seen with dorsal wall removed. B, labium and basal part of maxillae, ventral view, of *Hemaris thysbe*. C, labial palpus musculature of *Papilio glaucus*. D, same of *Danaus menippe*. E, same of *Pieris rapae*.

The musculature of the labium is limited to the palpi muscles. Berlese and Burgess have figured palpus muscles arising on the tentorium, but apparently did so by mistaking proboscis extensors for palpi muscles. In every moth and butterfly examined by the writer there were never more than two pairs of palpus muscles, and these arise either on the labium itself or on the hypostomal bridge. The articulation of the labial palpus with the head is so formed that little or no blood passes out into the palpus. If the palpus of a live butterfly is snipped off, it will be found that the walls of both the first and the second joints are barely moist inside. This, of course, greatly lightens the palpi.

The palpus musculature of *Danaus menippe* is illustrated in figure 12 D. Each palpus is supplied with two muscles, a levator (*lplp*) and a depressor (*dplp*). Nymphalidae usually have a pair of muscles for each palpus, although the depressor is often very weak. In the Papilionidae and the Pieridae there is no depressor muscle, but the levator is always well developed (fig. 12 C, E). In this case the levator arises either on the sclerotized *median plate* (MP) of the labium, or on the hypostomal bridge.

The presence or absence of labial palpus muscles is extremely variable in the other families. *Pronuba yuccasella* has no palpus muscles, nor does an *Agonopterix* sp. Each palpus of *Galleria mellonella* has a single large muscle. Geometridae show only a single palpus muscle or none at all. In the Arctiidae there is only a single muscle, usually arising on the hypostomal bridge. Sphingidae have either one or two pairs of palpus muscles, commonly only one. Saturniids and other extremely degenerate groups usually lack any palpus musculature, and the trembling motion of the palpi sometimes seen in this family is usually caused by the remnants of the proboscis extensors. However, *Basilona imperialis* has a single muscle in each palpus, as does also *Malacosoma americana*.

V. SUMMARY

1. The coiled proboscis of Lepidoptera is extended by means of blood pressure created in the stipes of each maxilla. This pressure is caused by three pairs of muscles, which by their contraction press the stipes against the head wall. Two pairs of these muscles arise on the anterior arms of the tentorium and the third pair arises on the gena.

2. The sucking pump is a compound organ, derived from the pharynx, the buccal cavity, and the cibarium. This is evidenced by these facts: (1) true pharyngeal dilators are inserted only in the posterior part of the pump; (2) muscles homologous with the compressors of the labrum are present in some Lepidoptera; and (3) the dorsal salivarium muscles arise on the pump floor, showing that the hypopharynx forms at least the anterior part of the floor.

3. There is no labial musculature except that of the palpi. There are generally two pairs of palpus muscles, but in many families only one pair, or none at all, may be found.

4. The area posterior to the labial palpi is bounded by the hypostoma, the hypostomal ridge offering an insertion for the ventral intersegmental muscles. A hypostomal bridge is sometimes present.

5. The anterior arms of the tentorium are well developed but lack dorsal arms. The posterior tentorial bridge is short and weak. The

great length of the hypostoma in Lepidoptera elevates the tentorium to a higher position in the head, with respect to other cephalic structures, than is common.

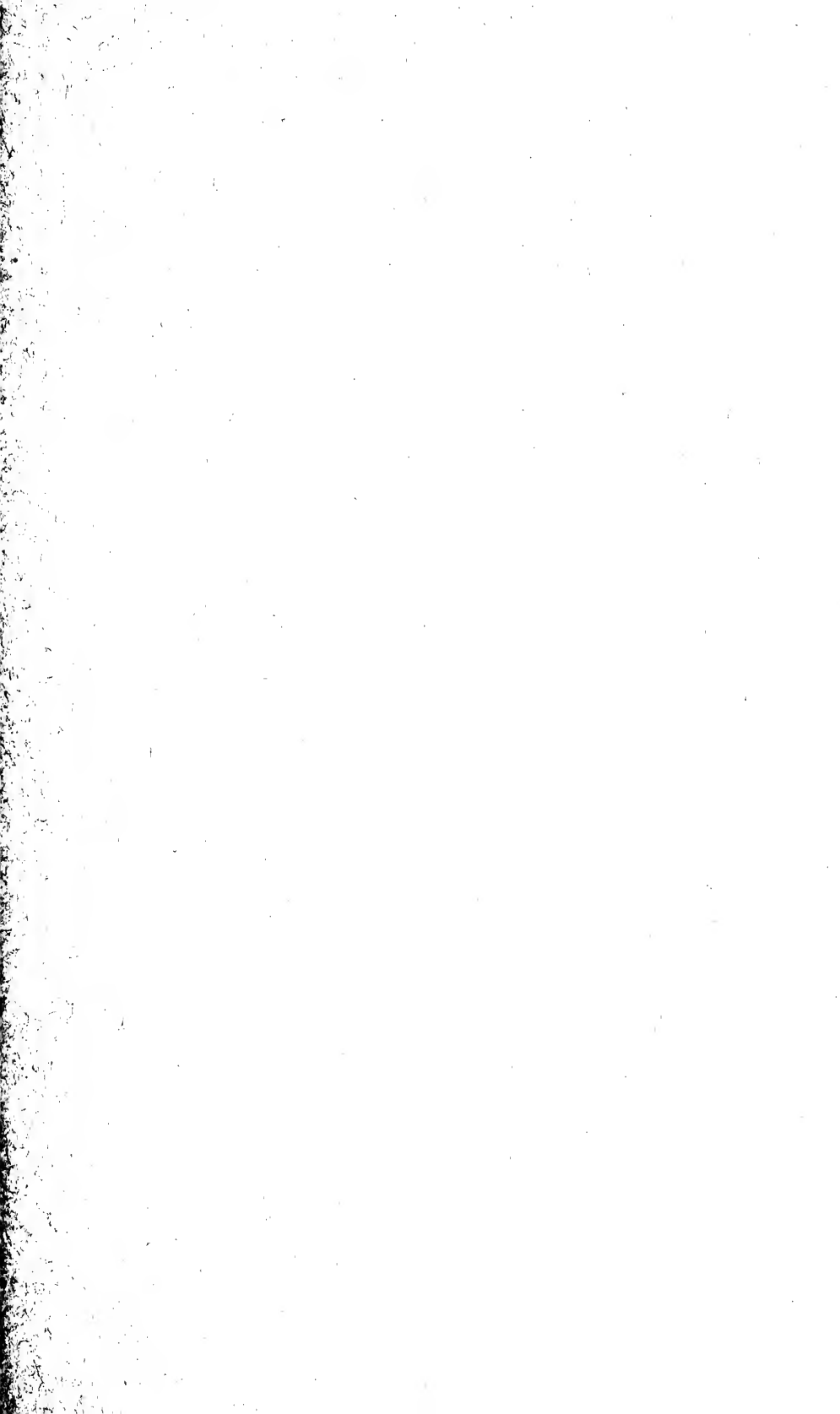
6. The antennal muscles arise on the anterior arms of the tentorium and vary in number from one to five pairs. They are always well developed, sometimes at the expense of other head structures and, in moths with obsolete feeding structures, are often the only functional muscles within the head.

ABBREVIATIONS USED ON THE FIGURES

<i>Ant</i> , antenna.	<i>Nv</i> , nerve.
<i>ant mcl</i> , antennal muscle.	<i>Oc</i> , occiput.
<i>Ant Nv</i> , antennal nerve.	<i>OcR</i> , occipital ridge.
<i>AR</i> , antennal ridge.	<i>ocs</i> , occipital suture.
<i>AT</i> , anterior tentorial arms.	<i>Oc</i> , oesophagus.
<i>at</i> , invagination of anterior arm.	<i>OIm</i> , oral valve muscle.
<i>atp</i> , anterior tentorial proboscis extensor.	<i>PBm</i> , proboscis base muscles.
<i>BuC</i> , buccal cavity.	<i>PC</i> , pressure chamber.
<i>Br</i> , brain.	<i>Phy</i> , pharynx.
<i>Cd</i> , cardo.	<i>Plf</i> , pilifer.
<i>Clp</i> , clypeus.	<i>Plp</i> , palpus.
<i>cp</i> , cranial proboscis extensor.	<i>Poc</i> , postocciput.
<i>Cv</i> , cervix.	<i>PoR</i> , postoccipital ridge.
<i>dlbc</i> , dilator of buccal cavity.	<i>pos</i> , postoccipital suture.
<i>dlcb</i> , dilator of cibarium.	<i>Prb</i> , proboscis.
<i>dplp</i> , depressor of palpus.	<i>Prb Ext</i> , proboscis extensor.
<i>dlphy</i> , dilator of pharynx.	<i>Prtl</i> , parietal.
<i>E</i> , eye.	<i>PT</i> , posterior tentorial arms.
<i>fm</i> , food meatus.	<i>pt</i> , invaginations of posterior arms.
<i>Fr</i> , frons.	<i>ptp</i> , posterior tentorial proboscis extensor.
<i>Fr Con</i> , frontal connective.	<i>rao</i> , retractor of mouth angles.
<i>Fr Gng</i> , frontal ganglion.	<i>rhphy</i> , retractor of hypopharynx.
<i>HBr</i> , hypostomal bridge.	<i>rn(RNv)</i> , recurrent nerve.
<i>Hphy</i> , hypopharynx.	<i>ts</i> , anterior salivarium muscle.
<i>HphyR</i> , hypopharyngeal ridge.	<i>zs, zs</i> , posterior salivarium muscle.
<i>HR</i> , hypostomal ridge.	<i>SID</i> , salivary duct.
<i>hs</i> , hypostomal suture.	<i>Slv</i> , salivarium.
<i>Hst</i> , hypostoma.	<i>sm</i> , salivary meatus.
<i>Lb</i> , labium.	<i>Soc Gng</i> , suboesophageal ganglion.
<i>Lb Plp</i> , labial palpus.	<i>SP</i> , sucking pump.
<i>lplp</i> , levator of palpus.	<i>SR</i> , stipital ridge.
<i>lpm</i> , lateral pump muscle.	<i>St</i> , stipes.
<i>Lrm</i> , labrum.	<i>tpm</i> , transverse pump muscle.
<i>MP</i> , median plate.	<i>Tr</i> , trachea.
<i>Mth</i> , mouth.	<i>v/v</i> , valve.

REFERENCES

- BERLESE, A.
1910. Gli insetti, vol. 1. Milan.
- BURGESS, E.
1880 a. The structure and action of a butterfly's trunk. *Amer. Nat.*, vol. 14, pp. 313-319.
1880 b. Contribution to the anatomy of the milkweed butterfly. *Anniv. Mem. Boston Soc. Nat. Hist.*
- JOBLING, B.
1929. A comparative study of the structure of the head and mouthparts in the Streblidae (Diptera Pupipara). *Parasitology*, vol. 21, pp. 417-444.
- KELLOGG, V. L.
1893. The sclerites of the head of *Danaus archippus*. *Kansas Univ. Quart.*, vol. 2, pp. 51-59.
1895. The mouthparts of the Lepidoptera. *Amer. Nat.*, vol. 29, pp. 546-556.
- KIRBACH, P.
1883. Über die Mundwerkzeuge der Schmetterlinge. *Zool. Anz.*, vol. 6, pp. 553-558.
- SNODGRASS, R. E.
1932. Evolution of the insect head and the organs of feeding. *Ann. Rep. Smithsonian Inst. for 1931*, pp. 443-489.
1935. *Principles of insect morphology*. McGraw-Hill Book Co., New York.
- TILLYARD, R. J.
1923. On the mouth-parts of the Micropterygoidea. *Trans. Ent. Soc. London*, vol. 71, pp. 181-206, 12 figs.
- WEBER, H.
1924. Das Thorakalskelett der Lepidopteren. Ein Beitrag zur vergleichenden Morphologie des Insektenthorax. *Zeitschr. Anat. und Entwickl.*, vol. 73, pp. 277-331, 9 figs.





SMITHSONIAN MISCELLANEOUS COLLECTIONS
VOLUME 97, NUMBER 5

THREE PICTOGRAPHIC AUTOBIOGRAPHIES
OF SITTING BULL

(WITH 46 PLATES)

BY
M. W. STIRLING
Chief, Bureau of American Ethnology



(PUBLICATION 3482)

CITY OF WASHINGTON
PUBLISHED BY THE SMITHSONIAN INSTITUTION
JULY 22, 1938



Photograph by Barry

SITTING BULL

SMITHSONIAN MISCELLANEOUS COLLECTIONS
VOLUME 97, NUMBER 5

THREE PICTOGRAPHIC AUTOBIOGRAPHIES OF SITTING BULL

(WITH 46 PLATES)

BY

M. W. STIRLING

Chief, Bureau of American Ethnology



(PUBLICATION 3482)

CITY OF WASHINGTON
PUBLISHED BY THE SMITHSONIAN INSTITUTION
JULY 22, 1938

The Lord Baltimore Press
BALTIMORE, MD., U. S. A.

THREE PICTOGRAPHIC AUTOBIOGRAPHIES OF SITTING BULL

BY M. W. STIRLING

Chief, Bureau of American Ethnology

(WITH 46 PLATES)

INTRODUCTION

The name of Sitting Bull will probably always remain as the best known of any American Indian. Whether or not this preeminent place is deserved, it is a fact that more has been printed about him than any other Indian and his name has most intrigued the popular imagination. Part of this notoriety resulted from the fact that he was a prominent and influential Indian during a crucial period in the history of his tribe and partly from the fact that during the latter years of his life he was exploited, both in this country and abroad, in a manner calculated to bring his achievements in a highly colored manner before the general public.¹

It is not the purpose of this introduction to outline the career of Sitting Bull. This has been adequately done by a number of biographers, and the interested reader is referred to the attached selected bibliography.

There is no question concerning the fact that Sitting Bull was a great man, in spite of the fact that many of his contemporaries attempted to belittle his character. It is true, however, that the prominence he later achieved in the popular mind was partly due to circumstances which gave unusual publicity to his career.

In view of his status with the government, Sitting Bull was always reluctant to speak with white men regarding his personal adventures. However, in keeping with the custom of his people, he was proud of his war exploits and kept a careful record of them.

¹ In an unpublished manuscript on Sioux names by the famous scout and interpreter, E. H. Allison, the author says of the Indian name of Sitting Bull, Tatanka Yotanka; "Sitting Bull's totem was a bull standing in a defiant attitude, which clearly expressed the meaning of his name, 'The Bull in Possession,' 'The Conquering Bull,' 'The Bull of Occupation,' 'The Sitting Bull.'"

I. THE KIMBALL PICTOGRAPHIC RECORD

When Sitting Bull recounted his honors at the dance following the Sioux victory over the Crow in 1870, Frank Grouard, who was present, states that at this time Sitting Bull was entitled to 63 *coups*.² About this same time Sitting Bull made his pictographic record after the usual manner of the Plains Indians, representing the feats which entitled him to special credit among the Indians. This set of drawings he gave to his adopted brother, Jumping Bull, who placed with them a pictographic record of his own. While these drawings were in the possession of Jumping Bull, Four Horns copied 55 of them, including 40 from the record of Sitting Bull and the remainder from that of Jumping Bull. In some manner, not yet explained, these copies fell into the hands of another Indian who brought them to Fort Buford, where they eventually came into the possession of Assistant Surgeon James Kimball in August 1870. The fate of the original drawings from which this set was made is not known, although Sitting Bull stated that they were still in the possession of Jumping Bull as late as 1881. According to Col. H. M. Morrow, his father, also Col. H. M. Morrow, who was with Dr. Kimball, procured an identical set at the same time. These copies were both drawn on roster sheets of the Thirty-first United States Infantry. The copy retained by the Morrow family was destroyed in San Francisco in the great fire of 1906. The copy obtained by Dr. Kimball was deposited by him, together with explanations of the pictures obtained at the time from other Indians, with the Medical Director's Office, Department of Dakota, on March 14, 1871. The same year they were transferred to the Army Medical Museum in Washington, D. C. On May 15, 1915, Dr. D. S. Lamb of the Army Medical Museum transferred them to the archives of the Bureau of American Ethnology, where they are at the present time.

From time to time this pictographic record has attracted considerable attention, but it has been reproduced only in part, and the supporting documents concerning it have never before been published.

Although the name of Sitting Bull had already become well known to the whites, he did not become a figure of outstanding national interest until after the annihilation of General Custer and the Seventh Cavalry, June 25, 1876, in which battle Sitting Bull participated.

² De Barthe, 1894, p. 105.

As news concerning the details of the Custer defeat slowly filtered in from the northern plains, newspaper men realized that they had the biggest news story since the Civil War. The fact that the colorful Custer, who had become something of a national idol, was the central figure in the tragic affair, made the story ideal from the standpoint of the journalists. In search of material which could be tied in with the Custer fight, a Washington correspondent learned of the existence of the copy of Sitting Bull's autobiography, then in the Army Medical Museum. Sitting Bull was known to have participated in the battle. Here then was the perfect nucleus for a follow-up story. On July 6, 1876, the New York Herald published a highly colored account of the pictographic record, neglecting to note that the autobiography was not the original handiwork of Sitting Bull. The record was cited as proof of Sitting Bull's cruelty, lust for battle and vainglorious boastfulness. This story was a huge journalistic success. It was copied and revamped by newspapers and magazines throughout the United States. Sitting Bull, who heretofore in the public mind had been but one of a group of hostile chiefs resisting the westward advance of the whites, now became Public Enemy Number 1 and a character of outstanding interest.

Apparently, an introduction written by Dr. Kimball formerly accompanied the explanatory index and the Williamson letter of verification which are now with the pictographic record.

The news release from Washington of July 6, 1876, as published by the New York Herald says:

Among the many ghastly souvenirs preserved at the Army Medical Museum of this city is an autobiography of Sitting Bull, gotten up in the highest style of the art of savage picture history, and telling, in fifty-five drawings or sketches, the story of his life down to 1870. Each picture is rudely outlined in ink, the men, horses and other objects being such as children would make. Many of them are partly filled in with red and blue colors as if Sitting Bull had at some time got possession of one of the red and blue pencils so well known in newspaper offices, and with it elaborated his pictorial efforts. Blood or a wound is indicated by a red blotch with streamers falling down from it. The blue is used generally in indicating the white man's pantaloons. Each picture is made on a sheet of paper eight by ten inches, and is pasted into a book of blank leaves, such as are used for a scrap book. By holding the sheets up to the light it is seen that they are the muster-roll blanks of the 31st United States Infantry, of which Col. de Trobriand was the commandant. The papers probably fell into Sitting Bull's hands at the evacuation of a camp, or, as is more likely, were stolen by him during a visit to some of our outposts. Sitting Bull is not at all modest in committing to posterity the story of his great deeds. Whether it be the scalping of a soldier in battle or the sly theft of a mule, he brags equally of his prowess in his curious autobiography. This literary work, which is now likely to be famous, fell into the hands of Assistant Surgeon

James C. Kimball, of the army, in the month of August, 1870, while he was stationed at Fort Buford, Dakota Territory. He had the pictures translated, and sent them, with the translation and an index, to the Curator of the Army Medical Museum, Washington, Surgeon George A. Otis, United States Army, who has filed them in book shape, among the archives of the Museum. The introduction, written by Dr. Kimball goes on to say that the autobiography contains a description of the principal adventures in the life of Sitting Bull, who is an Unk-pa-pa chief. It was sketched by himself in the picture language, in common use with the Indians. Since the establishment of Fort Buford, in 1866, Sitting Bull, at the head of from sixty to seventy warriors, had been the terror of mail-carriers, wood-choppers and small parties in the vicinity of the post and from 100 to 200 miles from it either way, up and down the Missouri River. During the time from 1866 to 1870, when the autobiography was written, this band had several times captured and destroyed the mail and had stolen and run off over 200 head of cattle and killed near a score of white men in the immediate vicinity of the fort. The Unk-pa-pas are a tribe of the great Sioux Nation, living in the Yellowstone and Powder River countries.

The book was brought into Fort Buford by a Yanktonnais Sioux, and offered for sale and purchased for \$1.50 worth of provisions. The Indian gave conflicting statements regarding the manner in which he came into possession of the book, exciting suspicion that he had stolen it from Sitting Bull, who in his turn, undoubtedly stole the book in blank from the whites.

In an article over the name of Porte Crayon published in the supplement to Harper's Weekly of July 29, 1876, the editor says:

About the year 1870 a collection of MS. drawings, put up in book form, bearing the autograph of Sitting Bull and exhibiting a record of his exploits and adventures, was brought into Fort Buford by a Yanktonnais Sioux and sold for a dollar and fifty cents worth of provisions. When cross-questioned regarding the ownership of the book, the Indian shuffled and prevaricated so as to confirm the belief that he had stolen it from Sitting Bull himself. The authenticity of the work, with its general historical accuracy, is confirmed by Assistant Surgeon James C. Kimball, U.S.A., who, with the aid of interpreters, Indians, and others versed in the picture-language of the Northwestern tribes, wrote a detailed explanation of the scenes represented, accompanied by a brief sketch of the warrior-artist's life. The book was then forwarded to the Superintendent of the Army Medical Museum at Washington, who placed it in the hands of the present editor.

The series consists of fifty-five designs, drawn on the blank side of printed rosters of the Thirty-first United States Infantry, of uniform size (about eight by ten inches), clearly outlined with a pen and a brown ink resembling sepia. There is no attempt at shading, but the outlines are filled in with flat tints, very crudely laid on, with red and blue chalk, yellow ochre, green, and the same brown ink or pigment used in the outlines. The coloring, which is quite appropriate in the dress and trappings of the human figures, is rather florid in the animals. Thus while there seems to be great care in showing the characteristic spots and markings of the horses and mules, the sorrels are represented with bright yellow, the grays with blue, the bays red, and the browns and blacks with the aforesaid brown ink.

This coloring, however, serves to impart life and meaning to the designs, to relieve the groupings from confusion, and is sometimes so arranged as to produce quite an artistic effect of *chiaro-oscuro*. It may be further noted that there is no attempt at foreshortening, the objects and figures being all shown in flat profile, and without exception, all looking and moving in the same direction, that is, from right to left.

Of all the objects presented by the artist, the figure of the buffalo bull is elaborated with the most intelligent and loving minuteness. The horses and mules are drawn with a free and well-assured hand, with a tendency to mannerism, relieved somewhat by distinctive character in color, markings, and details. He is least happy in his delineations of the human figure, draperies, and accoutrements, although in some scenes his attitudes are spirited and his costumes sufficiently marked to enable us to identify the sex and country of those who have had the honor to sit for their portraits to this distinguished limner.

The information in the two foregoing newspaper accounts concerning the manner in which the pictographic record was obtained at Fort Buford presumably was obtained from Dr. Kimball's now missing introduction. The article published by Harper's Weekly reproduces 11 of the drawings with a rather detailed description of the set based partly on the Kimball index and partly upon speculation by the editor.

As already indicated, the pictures are drawn on the reverse side of loose-leaf roster pages of the Thirty-first United States Infantry. The numbers were subsequently placed on them arbitrarily without regard to the actual chronology of the events described.³

In 1881 the pictures, together with the Kimball index, were forwarded through Col. George S. Andrews to Rev. John P. Williamson, missionary with the Sioux, who showed them to Sitting Bull for purposes of verification. The results obtained from this interview are explained in the following letter:

FORT RANDALL, DAKOTA TER.
Dec. 12, 1881.

COL. GEO. L. ANDREWS,
25 U. S. Infantry,
Commanding Post,

SIR:

I have the honor to state that in connection with Capt. G. Lawson, I interviewed Sitting Bull in regard to the supposed "Hyeroglyphic Autobiography" of himself, contained in pictured sketches, numbered 1 to 55, obtained by Jas. C. Kimball, Ass't. Surgeon, U.S.A., in the year 1870.

³ Vestal, in describing them, has placed them in what he considers to be the order in which the different feats took place.

Sitting Bull immediately recognized the pictures as scenes from his early life, with the exception of Nos. 39 to 51, and 53 and 54, which he said were not his, but were adventures of his brother Jumping Bull.

As to the scenes from his own life, he says these are all true scenes, and he drew a similar set many years ago and gave them to his brother Jumping Bull. He saw his brother last summer and understood from him that he still had them. He thinks therefore that this set must be a copy of the one he made, and has been drawn off by some Indian, he does not know by whom. He could tell perhaps by seeing his brother who is at Standing Rock.

Sitting Bull verified in the main the Index accompanying the pictures.

No. 1 he says was his first feat, accomplished when he was fourteen years of age.

No. 10 he says was a Ree, who drops his gun and bow from fear. He was struck (for "coup") but not killed (no blood is shown). The scalp at the horses bridle, here and elsewhere, not being intended to represent the scalp of the enemy drawn.

No. 55 he says is not completed—should have his "name" (as he calls the sitting buffalo).

As to the particular history of each event recorded, we found Sitting Bull rather reserved, especially in regard to Scenes Nos. 11 to 26, and we could see that any narration he gave of the several events was colored by the circumstances of his present situation. And I would suggest that if a more full account of his war deeds is desired, a better time to secure it would be at some future date when his status is definitely determined.

Yours Respectfully,

(signed) JOHN P. WILLIAMSON,
Missionary.

In reproducing the drawings, the explanation of each is given exactly as written in the Kimball index in 1870. It should be borne in mind that these interpretations were furnished by Indians familiar with the career of Sitting Bull but not by the Sioux warrior himself.

For purposes of comparison these explanations are supplemented by the interpretations published by Vestal.⁴

No. 54 is missing from the set. This picture was one of the Jumping Bull series and represented an episode in the famous battle of 1870 between the Sioux and the Crow. The Kimball description says "Sitting Bull at the head of his band charges into a camp of Crows and kills thirty of them. (This happened in the winter of 1869-70.)"

⁴Vestal says, "For Sitting Bull's interpretations of these drawings, given in 1885, I am indebted to Mr. Seth C. Jones, Secretary, Municipal Art Commission, Rochester, N. Y."

No. 1

"Sitting Bull, a young man without reputation and therefore wearing no feather, engages in his first battle and charges his enemy, a Crow Indian who is in the act of drawing his bow, rides him down and strikes him with a 'coup' stick. Sitting Bull's autograph—a buffalo bull sitting on his haunches—is inscribed over him. His shield suspended in front has on it the figure of an eagle which he considers his 'medicine'—in the Indian sense of the term."⁵—KIMBALL.

⁵ See Williamson letter, p. 7. For detailed circumstances of this exploit, see Vestal, 1932, p. 13.

"1846. On Red Water. The boy Sitting Bull, as yet an unfledged warrior, is shown on horseback, charging an enemy whom he strikes with a *coup* stick. On his blue shield a black bird is painted, and four black-tipped eagle feathers flutter from the edges of the shield."—VESTAL.

No. 2

"Sitting Bull wearing a war bonnet is leader of a war party who takes a party of Crows consisting of three women and a man, so completely by surprise that the man has not time to draw his arrows from the quiver. Sitting Bull kills one woman with his lance and captures another, the man meanwhile endeavoring to drag him from his horse, from which it is supposed he is forced to desist by others of the war-party. The fate only of Sitting Bull and his victims is given in this history."—KIMBALL.

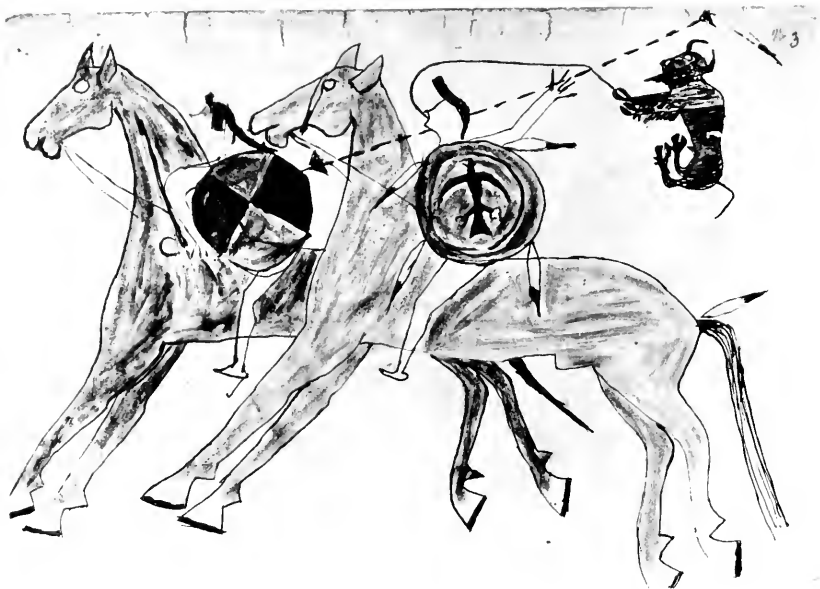
"1858. Rainy Butte. This picture commemorates the capture of three Crow women, at the time when Sitting Bull's father was killed. Sitting Bull carries the lance made for him by his parents, and wears a bonnet with horns and a long trail of eagle feathers. A Crow warrior is represented as trying to arrest his charge."—VESTAL.



1



2



3



4

No. 3

"Sitting Bull pursuing his enemy, a Crow Indian whom he strikes with his lance."—KIMBALL.

"1856. On Yellowstone River. Sitting Bull counts *coup* with his lance on a mounted Crow warrior who carries a shield and a gun. As required by the obligations belonging to his shield, Sitting Bull wears his hair in a knot like a horn on his forehead."—VESTAL.

No. 4

"Lances a Crow woman."—KIMBALL.

"1860. Sitting Bull counts *coup* on a Crow woman riding a mule. She turns to fend off his lance as he strikes at her. This happened when the Sioux encountered Crow hunters among the buffalo herds and Makes-the-Enemy killed two Crow women."—VESTAL.

No. 5

"Lances a Crow Indian."—KIMBALL.

"1853(?). Sitting Bull unhorses a Crow warrior with his lance. The story is well known, but no eye-witnesses now live, and the date and place are uncertain."—VESTAL.

No. 6

"Sitting Bull twice wounded, and unhorsed. His enemy, a Crow, at length killed by a shot in the abdomen and his scalp taken and hung on Sitting Bull's bridle."^a—KIMBALL.

^a Regarding the mention of scalps in this and succeeding pictures, see Williamson letter, p. 7.

"1856. On Porcupine Creek. Sitting Bull, shown wearing his Strong Heart bonnet and sash, crouches behind his shield and shoots a Crow chief through the belly, at the same time being wounded in the foot. Flame and smoke pour from the guns, and the wounds bleed freely. Sitting Bull's black war horse awaits its master in the background."—VESTAL.



5



6



7



8

No. 7

"In an engagement with the Crows, Sitting Bull mortally wounds one of the enemy and dropping his lance rides up and strikes him with his whip. The lines and dashes in the picture represent the arrows and bullets that were flying in the air during the combat."—KIMBALL.

"1861. Sitting Bull, amid a hail of enemy bullets, wounds a Crow warrior with his lance, then drops it and strikes him over the head with the heavy notched wooden handle of his quirt, which is decorated with a dangling kit-fox skin—the insignia of his Warrior Society. The Crow carries a quiver, and bleeds freely."—VESTAL.

No. 8

"Counts 'coup' on a Gros Ventre de Prairie, by striking him with his lance. Gros Ventre distinguished from Crow by manner of wearing the hair."—KIMBALL.

"1857. On the Missouri River. Winter. Sitting Bull, armed with a gun and wearing his Strong Heart and white blanket coat, strikes with his lance the Hohe lad whom he is to save and to adopt as his brother, named Jumping Bull, or Little Assiniboin."—VESTAL.

No. 9

"Lances a Crow Indian."—KIMBALL.

"1858. Near Rainy Butte. Sitting Bull lances and kills a Crow warrior, the slayer of his father in that very fight."^{5b}—VESTAL.

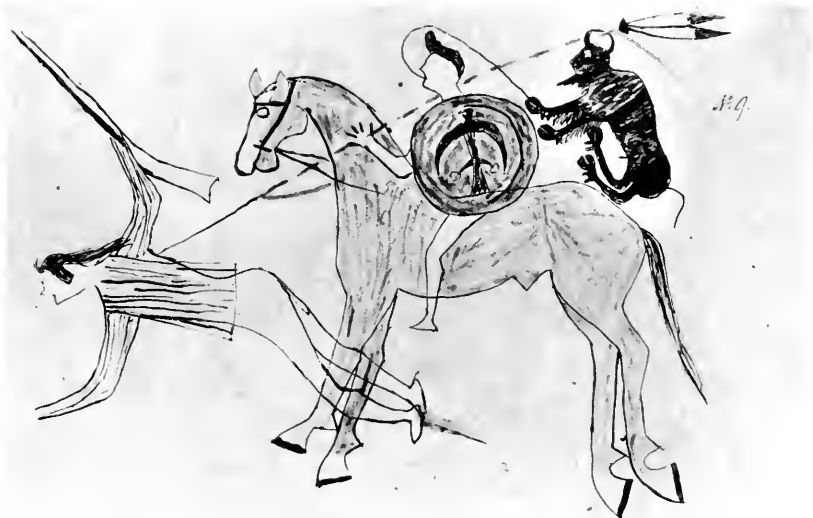
^{5b} For details see Vestal, p. 44.

No. 10

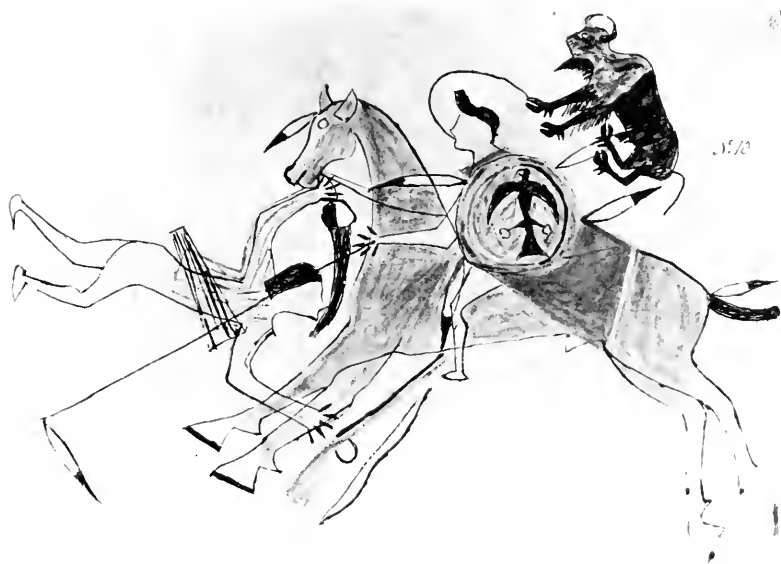
"A Crow Indian attempts to seize Sitting Bull's horse by the bridle. Sitting Bull knocks him down with a 'coup' stick, takes his scalp and hangs it to his bridle."⁶—KIMBALL.

⁶ Sitting Bull corrected this interpretation saying that his opponent is a Ree who drops his gun and bow from fear. The Ree was struck for coup but not killed (no blood is shown). See p. 7.

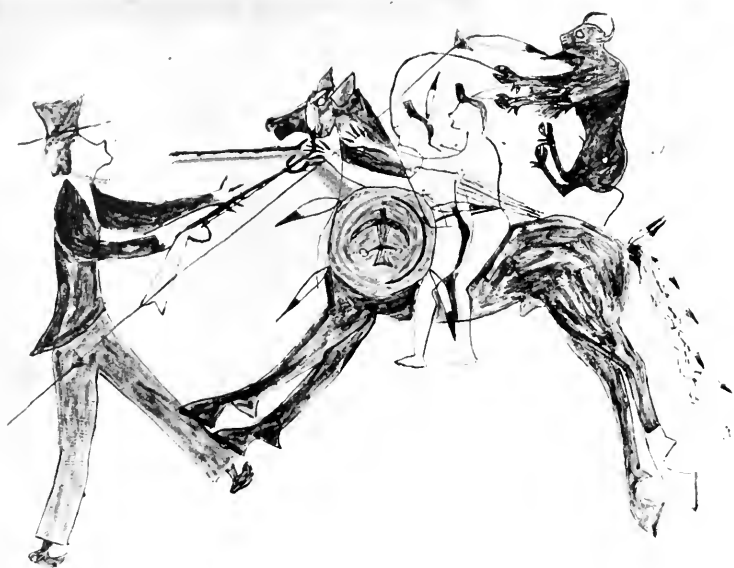
"1859. Near Fort Berthold. A Ree enemy grabs the bridle of Sitting Bull's horse. Sitting Bull kills him, and takes his gun and bow."—VESTAL.



9



10



11



12

No. 11

"Sitting Bull with his brother mounted behind him kill a white man—a soldier." ⁷—KIMBALL.

⁷When Williamson showed these pictures to Sitting Bull for verification, he found him unwilling to go into detail concerning his war exploits involving white opponents.

"1868. In a skirmish with white men Sitting Bull rescues his unhorsed companion Jumping Bull, takes him up behind, and charges a white man armed with a rifle. Jumping Bull, being armed with a long lance, is able to strike the white man first. Sitting Bull has to be content with the second *coup*."—VESTAL.

No. 12

"Counts 'coup' on a white man by striking him with a 'coup' stick." —KIMBALL.

"1868. Sitting Bull strikes a white man. This happened on the same warpath as the deed recorded in Fig. 11. Circling Hawk, now living, was leader of this war party."—VESTAL.

No. 13

"In a warm engagement with the whites, as shown by the bullets flying about, Sitting Bull shoots an arrow through the body of a soldier who turns and fires wounding Sitting Bull in the hip."—KIMBALL.

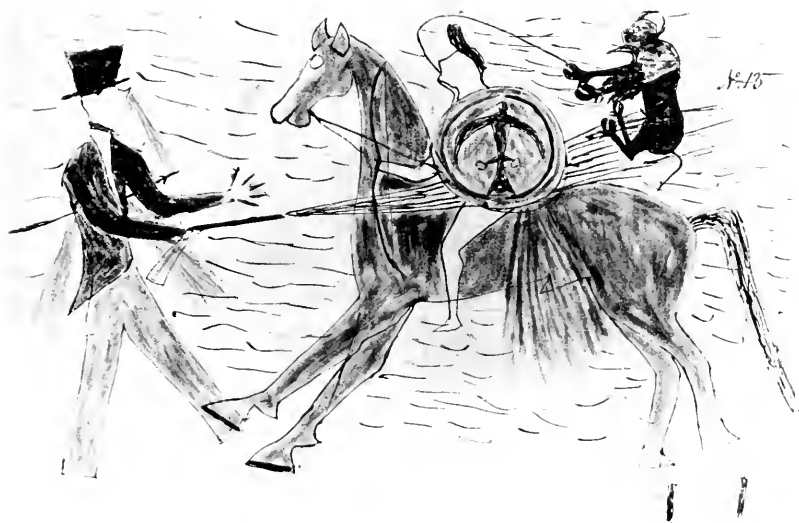
"1864. Near White Butte, on the Little Missouri River. Under heavy fire, Sitting Bull charges a white soldier. Though transfixed by an arrow from behind, and bleeding copiously from mouth and wounds, the brave soldier turns and shoots Sitting Bull through the buttocks, causing great loss of blood."^s—VESTAL.

^sThis episode is described in detail by Vestal. See Vestal, 1932, p. 64.

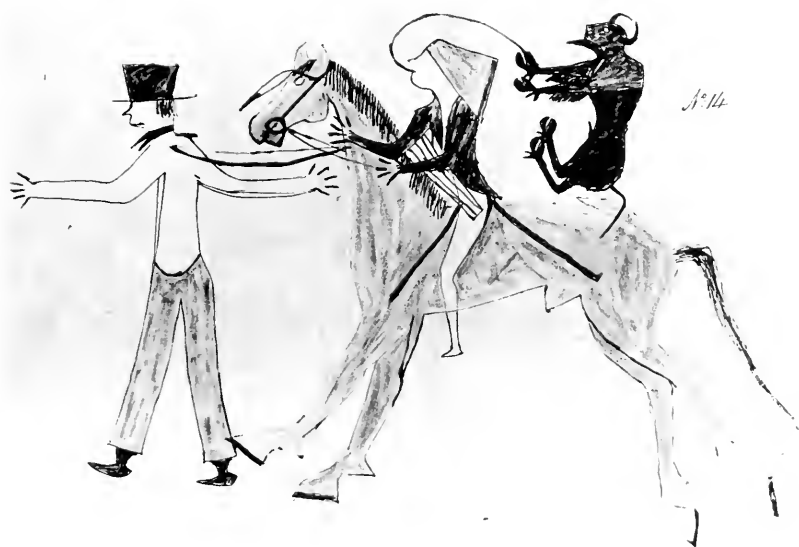
No. 14

"Sitting Bull counts 'coup' on a white man by striking him with his bow. Sitting Bull wears a jacket and bandanna handkerchief taken from some of his victims."—KIMBALL.

"1867-68 (winter). On the Montana Trail. Sitting Bull counts *coup* on a white man. In this affair Sitting Bull counted nine *coups*. This picture is followed by eight others showing the other *coups* struck. But as the drawings differ only in the details of the dress and persons of the white men, they have not been given here. Several of the white men were represented as having hair on their bodies—a thing considered loathsome by the Sioux."—VESTAL.



13



14



15



16

No. 15

“Sitting Bull counting ‘coup’ on a white man.”—KIMBALL.

No. 16

“Sitting Bull counting ‘coup’ on a white man.”—KIMBALL.

No. 17

"Sitting Bull counting 'coup' on a white man."—KIMBALL.

No. 18

"Sitting Bull counting 'coup' on a white man."—KIMBALL.



17



18



1:19

19



1:20

20

No. 19

“Sitting Bull counting ‘coup’ on a white man.”—KIMBALL.

No. 20

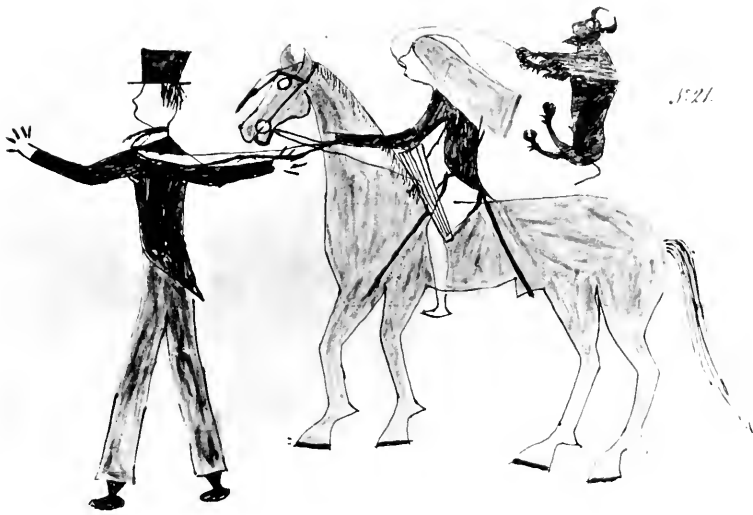
“Sitting Bull counting ‘coup’ on a white man.”—KIMBALL.

No. 21

“Sitting Bull counting ‘coup’ on a white man.”—KIMBALL.

No. 22

“Sitting Bull counting ‘coup’ on a white man.”—KIMBALL.



21



22



23



24

No. 23

"Sitting Bull shoots a frontiersman wearing a buckskin shirt, takes his scalp which he hangs on his own bridle and captures his horse. Sitting Bull wears a blanket."—KIMBALL.

"1863. Near Fort Totten, in the Devil's Lake country. Sitting Bull, wearing a red blanket, chases a mounted white man in a fringed buckskin coat, and shoots him between the shoulders. This was Sitting Bull's first white victim."—VESTAL.

No. 24

"Sitting Bull strikes a white soldier with his 'coup' stick, takes his scalp and his mule. Wears a war shirt."—KIMBALL.

"1863, June. The skirmish with General H. H. Sibley's wagon-train on the Missouri River, near the mouth of Apple Creek. Sitting Bull, facing a heavy fire, as shown by flying bullets, charges a mule-skinner armed with a blacksnake whip, counts *coup* on him, and makes off with a saddled mule."—VESTAL.

No. 25

"Counts 'coup' on a soldier, mounted with overcoat on, gun slung across his back, by riding up and striking with his riding whip."—KIMBALL.

"1867. On the Montana Trail. Sitting Bull overtakes a white man wearing an overcoat and armed with a rifle. Sitting Bull carries only a quirt, with which he strikes the fugitive. On his head Sitting Bull wears a bandanna taken from some enemy."—VESTAL.

No. 26

"Kills a white man and takes his scalp."—KIMBALL.

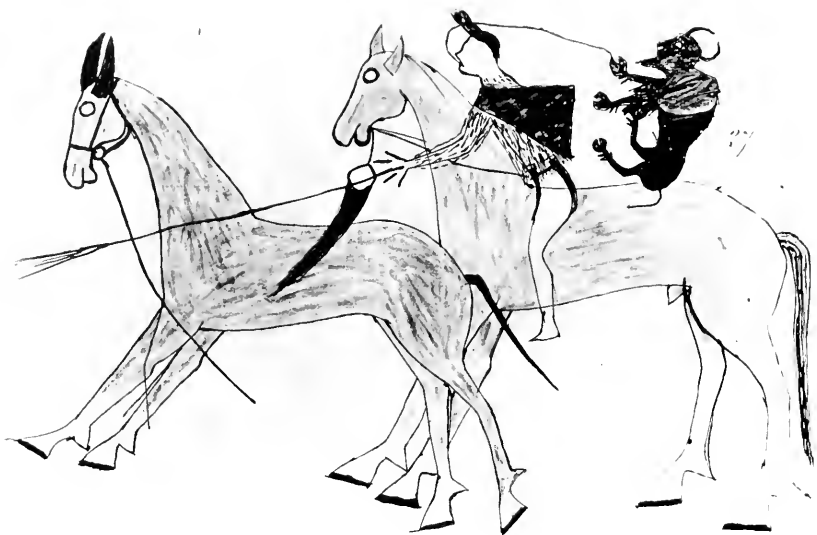
"1867. On the Niobrara River near the Missouri. Sitting Bull shoots a white man armed with a sawed-off shotgun. Sitting Bull carries a revolver, and is riding a rawhide saddle, made by his uncle."—VESTAL.



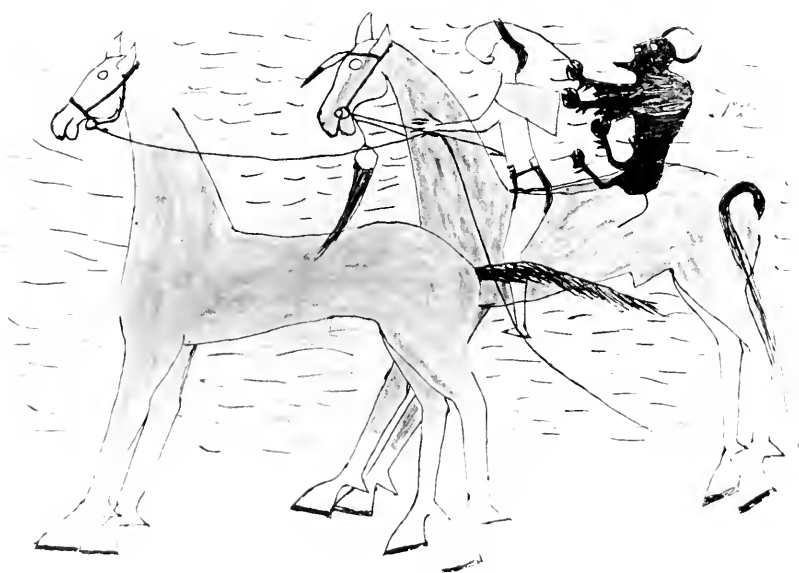
25



26



27



28

No. 27

"Captures a mule and a scalp."—KIMBALL.

"1865. North of the Black Hills. In a skirmish with the troops under Colonel N. Cole, of the Powder River Expedition, Sitting Bull runs off a slow pack-mule."—VESTAL.

No. 28

"In a warm engagement, captures a horse and a scalp."—KIMBALL.

"1865. On the Montana Trail. Under heavy fire from the soldiers, Sitting Bull captures a buckskin mare. He afterward gave her to his sister."—VESTAL.

No. 29

"Steals a mule."—KIMBALL.

"November 6, 1867. Fort Buford. In an attack on the woodcutters from the post, one soldier was killed, one wounded. Sitting Bull captures a fine brown Army mule with a black spot on the withers, off side. He gave the mule to his sister."—VESTAL.

No. 30

"Captures two horses in action."—KIMBALL.

"1864. Under fire, Sitting Bull takes from the soldiers a chestnut and a buckskin horse. The buckskin he trained to run buffalo, and then gave it to his sister. These horses were captured in the Badlands from General Sully's troops."—VESTAL.



29



30



31



32

No. 31

“Steals a horse.”—KIMBALL.

“1865. On the Montana Trail. Sitting Bull steals a fast buckskin war horse. He gave it to his adopted brother, Jumping Bull.”—VESTAL.

No. 32

“Steals and runs off a drove of horses from the Crows.”—KIMBALL.

“1863-64 (winter). Sitting Bull brings home nine Crow ponies: five bays, two blacks, one buckskin mule, and a little white mare. The mare he presented to his favorite sister, Pretty Plume.”—VESTAL.

No. 33

"In an engagement captures a government horse, and mule, and a scalp."—KIMBALL.

"1860. Amid a shower of bullets, which fill the air, Sitting Bull, riding his famous war horse Blackie, runs off two animals from a Crow camp. One of them is a branded Army mule, picked up or stolen by the Crows. These animals Sitting Bull gave for Brown Eyes, the girl who became his fourth wife."—VESTAL.

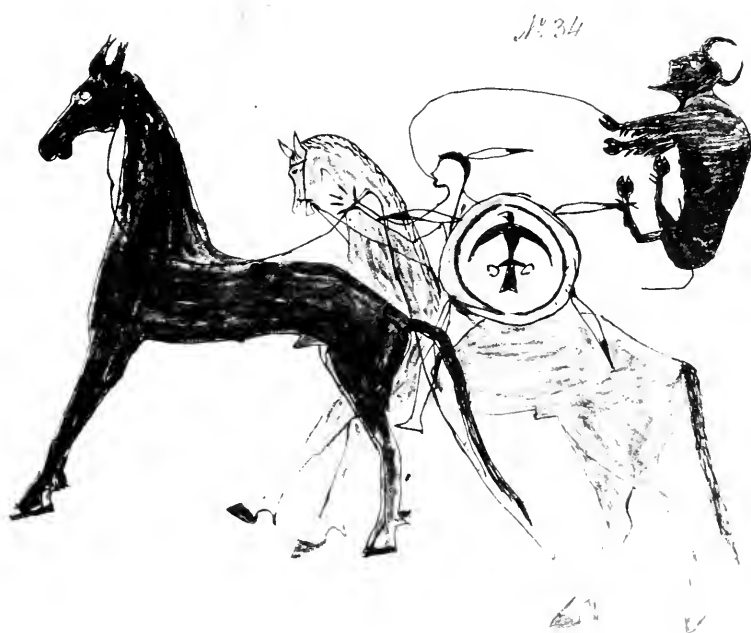
No. 34.

"Steals a horse."—KIMBALL.

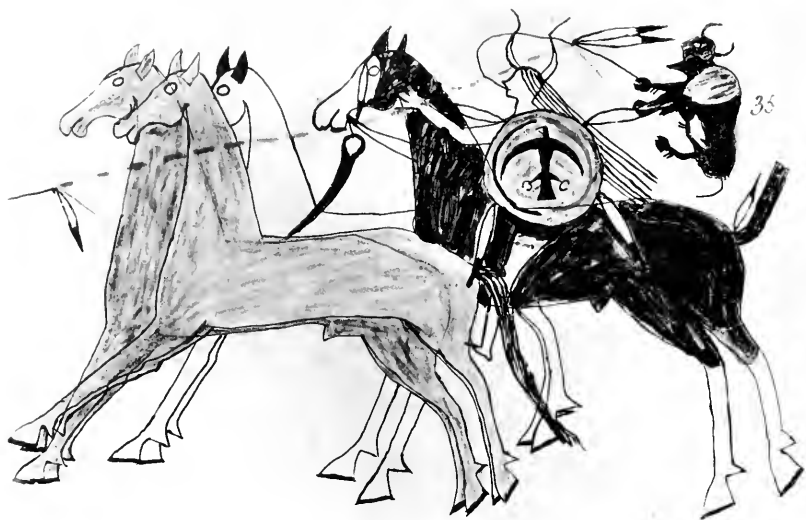
"1866. On the Montana Trail. Sitting Bull takes a horse with a split ear from white men."—VESTAL.



33



34



35



36

No. 35

"Captures three horses and a scalp."—KIMBALL.

"1866. Wearing his Strong Heart bonnet, and riding Blackie, Sitting Bull captures three Crow ponies; one bay, one black, one mouse-colored."—VESTAL.

No. 36

"Steals a drove of horses from the Crows."—KIMBALL.

"1862. Sitting Bull runs off a bunch of Crow ponies. Sitting Bull was such a noted horse-stealer that the old men say nobody can remember all his raids. Chief Charging Thunder stated that to his own knowledge Sitting Bull took horses from the Crows twenty times, sometimes as many as thirty head at a time."—VESTAL.

No. 37

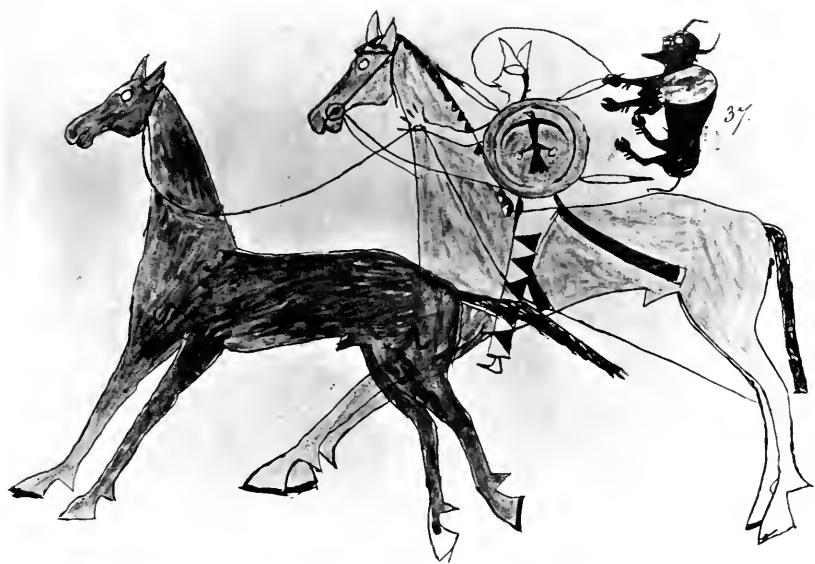
"Steals a government horse."—KIMBALL.

"1865. Wearing beaded leggins and a fur cap with earflaps, Sitting Bull runs off a horse belonging to the Powder River Expedition."—VESTAL.

No. 38

"Steals a drove of horses from the Crows."—KIMBALL.

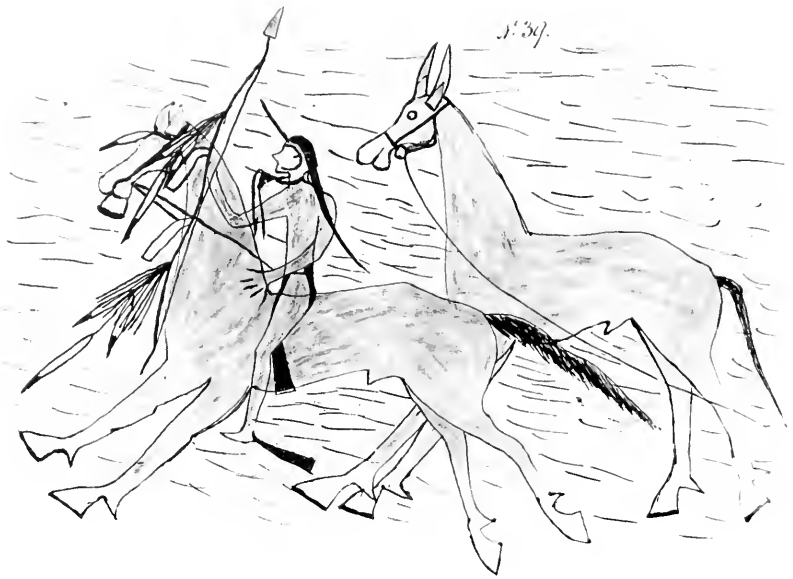
"1859-60. Wearing his Strong Heart bonnet, Sitting Bull runs off seven Crow ponies: two white, two black, one bay, one buckskin, and one mouse-colored."—VESTAL.



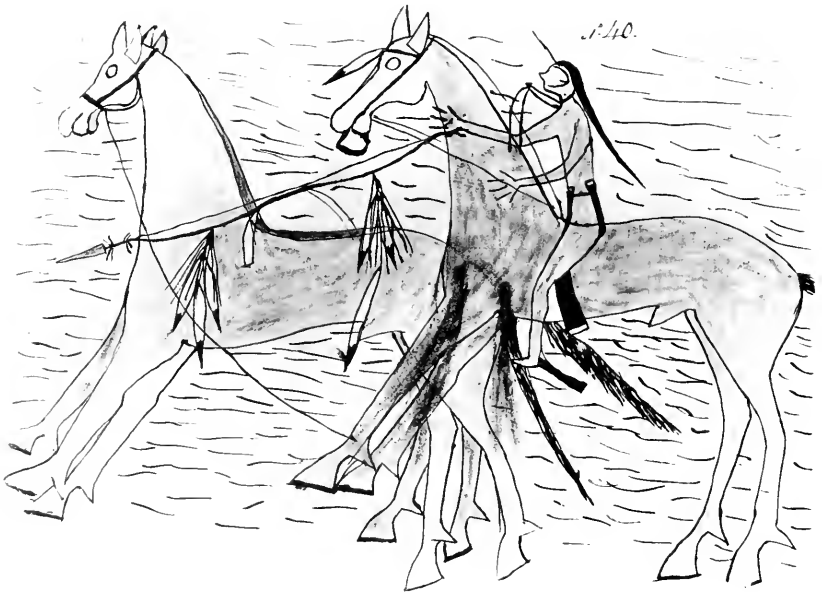
37



38



39



40

No. 39

"In an engagement captures a mule. Sitting Bull first appears here as Chief of the Band of Strong Hearts, to which dignity his prowess has raised him. The insignia of his rank—a bow having on one end a lance head—he carries in his hand." ⁹—KIMBALL.

⁹ This drawing actually depicts a feat of Jumping Bull the adopted son of Sitting Bull. See Williamson letter, p. 7.

No. 40

"Sitting Bull, Chief of the Band of Strong Hearts, captures two horses in an engagement in which his horse is wounded in the shoulder." ¹⁰—KIMBALL.

¹⁰ This drawing actually represents an exploit of Jumping Bull. It is erroneously attributed to Sitting Bull by Kimball. (See p. 7.)

No. 41

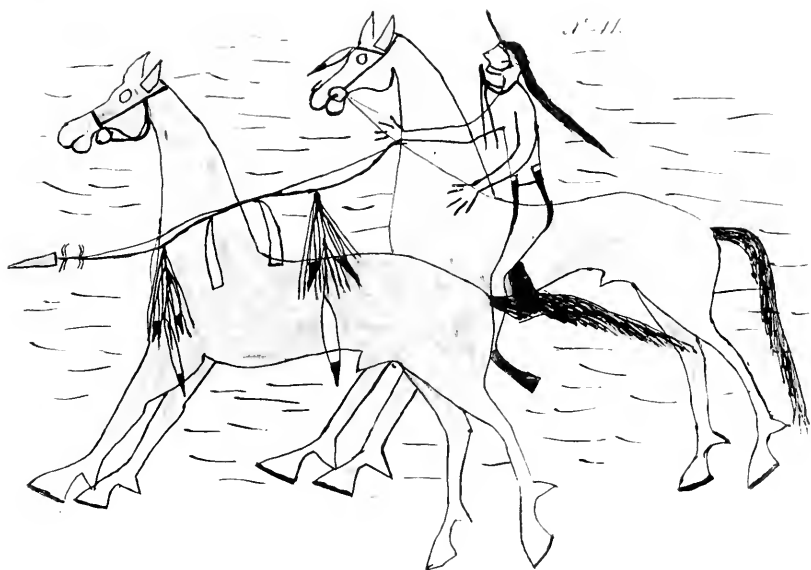
"Captures a horse in a fight."¹¹—KIMBALL.

¹¹ This drawing actually represents an exploit of Jumping Bull. It is erroneously attributed to Sitting Bull by Kimball. (See p. 7.)

No. 42

"Steals a mule."¹²—KIMBALL.

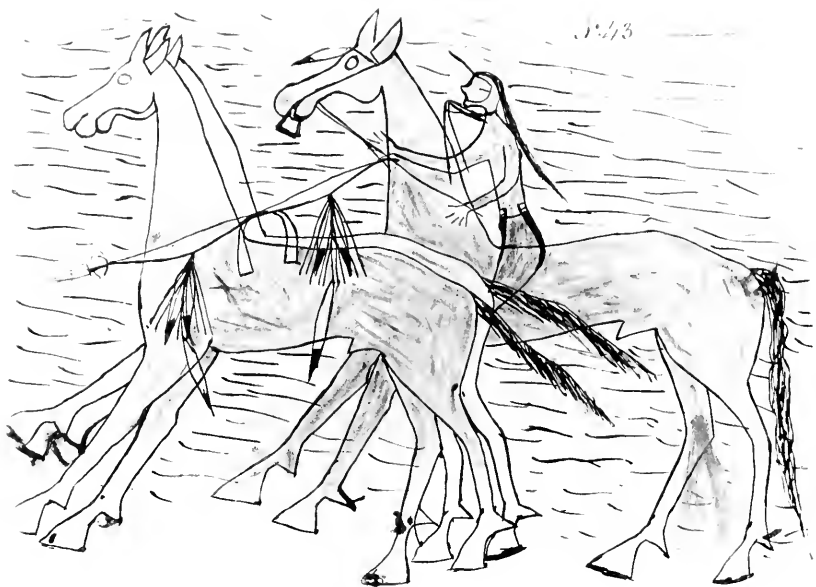
¹² This drawing actually represents an exploit of Jumping Bull. It is erroneously attributed to Sitting Bull by Kimball. (See p. 7.)



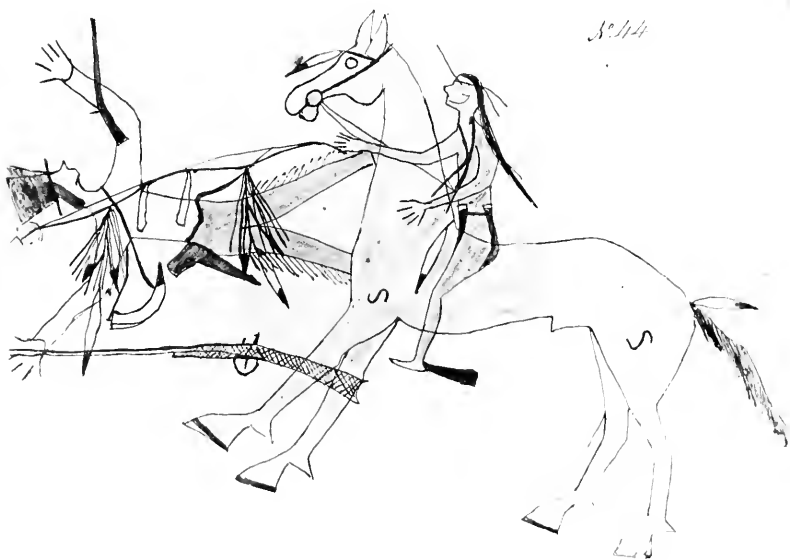
41



42



43



44

No. 43

“Captures two horses in a fight in which his horse is wounded in the leg.”¹³—KIMBALL.

¹³ This drawing actually represents an exploit of Jumping Bull. It is erroneously attributed to Sitting Bull by Kimball. (See p. 7.)

No. 44

“Mounted on a government horse, captures a white man.”¹⁴—KIMBALL.

¹⁴ This drawing actually represents an exploit of Jumping Bull. It is erroneously attributed to Sitting Bull by Kimball. (See p. 7.)

No. 45

"Steals two horses."¹⁵—KIMBALL.

¹⁵ This drawing actually represents an exploit of Jumping Bull. It is erroneously attributed to Sitting Bull by Kimball. (See p. 7.)

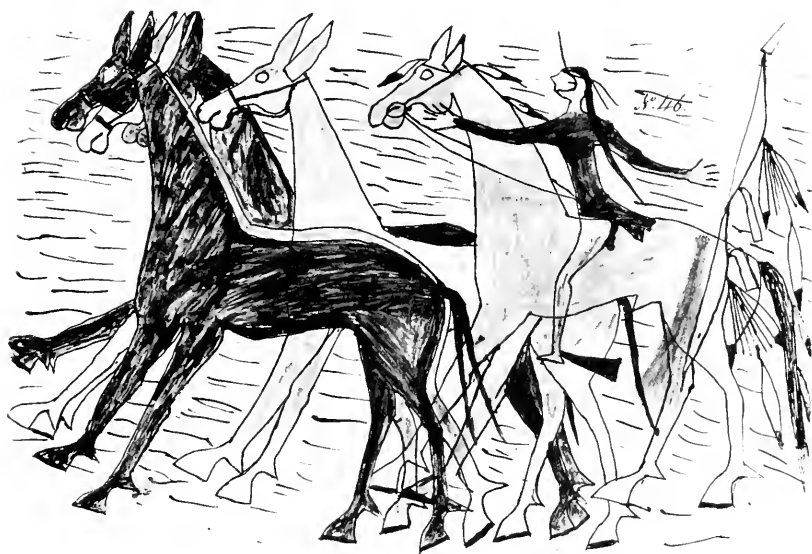
No. 46

"Captures four mules in a fight in which his horse is wounded in the hip."¹⁶—KIMBALL.

¹⁶ This drawing actually represents an exploit of Jumping Bull. It is erroneously attributed to Sitting Bull by Kimball. (See p. 7.)



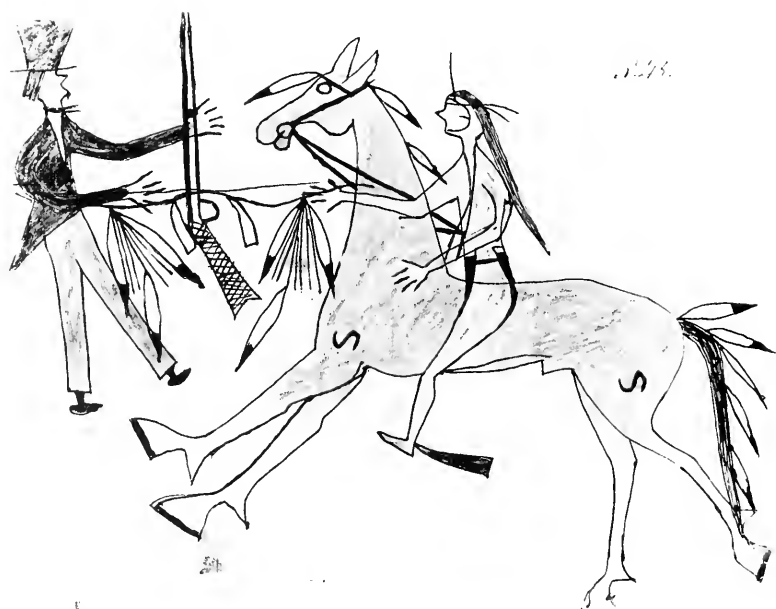
45



46



47



48

No. 47

“Counts ‘coup’ on white man.”¹⁷—KIMBALL.

¹⁷ This drawing actually represents an exploit of Jumping Bull. It is erroneously attributed to Sitting Bull by Kimball. (See p. 7.)

No. 48

“Counts ‘coup’ on white man.”¹⁸—KIMBALL.

¹⁸ This drawing actually represents an exploit of Jumping Bull. It is erroneously attributed to Sitting Bull by Kimball. (See p. 7.)

No. 49

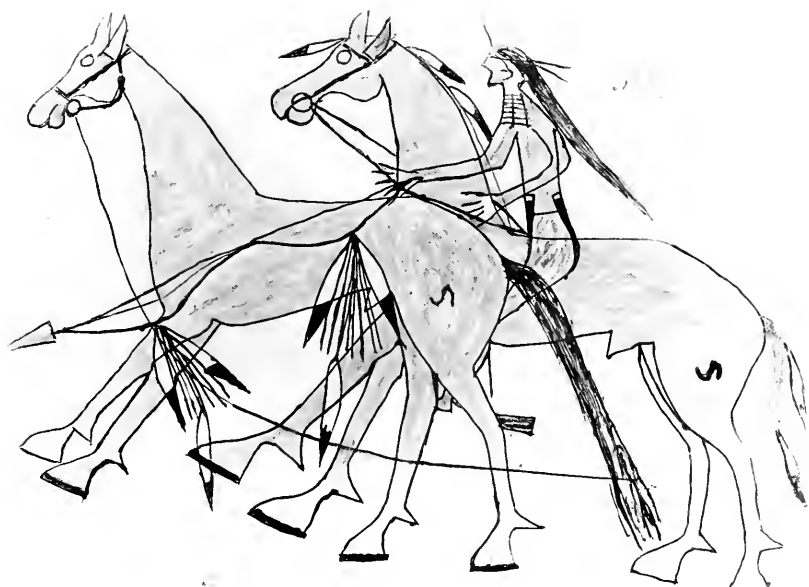
"Steals a government horse."¹⁹—KIMBALL.

¹⁹ This drawing actually represents an exploit of Jumping Bull. It is erroneously attributed to Sitting Bull by Kimball. (See p. 7.)

No. 50

"Fastens his horse to his lance driven into the earth and in a hand to hand fight kills a white man with his own gun. The black marks show the ground fought and trampled over."²⁰—KIMBALL.

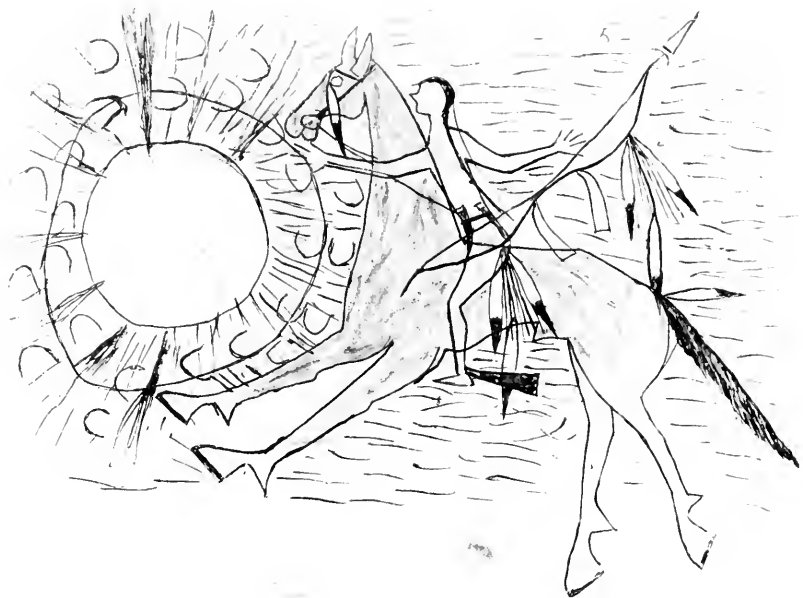
²⁰ This drawing actually represents an exploit of Jumping Bull. It is erroneously attributed to Sitting Bull by Kimball. (See p. 7.)



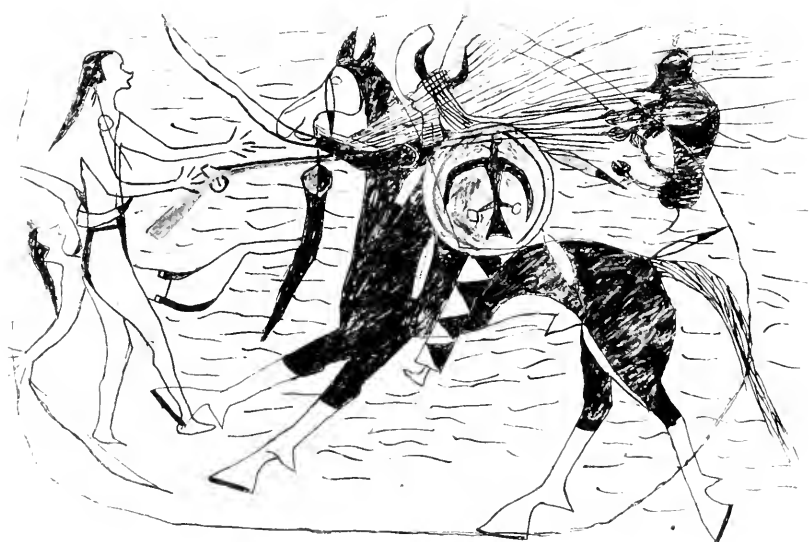
49



50



51



52

No. 51

"A fort into which his enemies the Crows, have retreated and from which they maintain a hot fire through which Sitting Bull charges the fort."²¹—KIMBALL.

²¹ This drawing actually represents an exploit of Jumping Bull. It is erroneously attributed to Sitting Bull by Kimball. (See p. 7.)

This apparently represents the feat of Jumping Bull performed at Spoon Horn Butte, where he drew the fire of the Crows in order to empty their guns before the Sioux charged. This exploit is described in Vestal, 1932, p. 116.

No. 52

"In a fight with the Crows, Sitting Bull kills and scalps one Indian, and counts 'coup' on another who fired at him barely missing him."²²—KIMBALL.

²² For details concerning this exploit see Vestal, 1932, chap. 16.

"1869. Near the Big Dry. An incident of the battle in which the thirty Crows were killed. Sitting Bull, wearing a horned bonnet and beaded leggings, charges the rocky barrier (indicated by the circle), and counts *coup* upon a Crow, who fires in his face, but misses. The air is full of flying lead."—VESTAL.

No. 53

"Steals a drove of mules."²³—KIMBALL.

²³ This drawing actually represents an exploit of Jumping Bull. It is erroneously attributed to Sitting Bull by Kimball. (See p. 7.)

No. 55

"Kills one Crow and counts 'coup' on two others, who run from him disgracefully."²⁴—KIMBALL.

²⁴ Sitting Bull stated to Williamson that this picture is incomplete. It should carry his "name" glyph. (See p. 7.)

"This, the last of the series, is incomplete, and lacks the picture of the seated buffalo, which should identify Sitting Bull. However, the shield is enough to serve that purpose. Sitting Bull himself explained that this unfinished sketch represented a fight with the Crows in which he killed one and counted *coup* on two others, who ran from him disgracefully. The date and place of this fight are unknown."—VESTAL.



53



55

II. THE SMITH PICTOGRAPHIC RECORD

In June 1923, through the generosity of Mr. Robert A. Smith, the Bureau of American Ethnology archives were enriched by another Sitting Bull document of even greater interest. This consists of a later Sitting Bull pictographic autobiography drawn by the great Sioux warrior himself. Although it contains drawings of only 22 exploits, it is well documented, and the explanations of the drawings were given by Sitting Bull at the time the pictures were made.

The drawings were made with a pencil on the pages of an army ledger book, and colored by means of water-color paint. The human figures are rather crudely drawn in the usual Plains Indian style, but Sitting Bull shows his individuality even in the field of art, by the manner in which the horses are depicted. Departing from the general Plains Indian style of representing horses in a slender and much conventionalized fashion, he draws his horses realistically and in a well rounded manner. The various horses shown are so conscientiously delineated that some of them can be recognized from descriptions of Sitting Bull's favorite mounts given by Vestal and others.²⁵

In the Four Horns copy of Sitting Bull's autobiography of 1870, the warrior is always identified by his name glyph in the form of a seated buffalo. At the time the present picture record was made, Sitting Bull had learned to write his name, and his signature accompanies each drawing in the place of the buffalo.

The following letter from Mr. Smith accompanied the book of pictures and the documents concerning them.

²⁵ Bob Davis, the well known newspaper writer, informed the author that in an interview in 1931, he learned that Rudolph Cronau was sent to America by the *Gartenlaube*, a weekly periodical published in Leipzig, to cover the Indian wars as illustrator. In 1881 the artist made the acquaintance of Sitting Bull shortly after his surrender at Fort Buford. Sitting Bull was much interested in watching Cronau make his sketches and wishing to gain the friendship of the Sioux leader, Cronau spent some time in teaching him to draw. This very probably accounts for the sophisticated and un-Indian appearance of the horses drawn by Sitting Bull.

ROBERT A. SMITH
430 S. Garden Street
South Bellingham, Wash.

June 20, 1923.

SMITHSONIAN INSTITUTION
Washington, D. C.

GENTLEMEN :

I am sending with this a book of paintings by Sitting Bull, with interpretation of same, letters from Wallace Tear, Lieut. 25th Infantry U.S.A. to my father, General John C. Smith, which explain themselves. Lieut. Tear was a soldier in the 96th Regt. Infantry—Illinois U.S.V. 1860-65.

My father was Captain, Major, Lieutenant Colonel, Brevet-Colonel 96th Regt., and Brevet Brig. General. At the close of the war he was able to get a commission in the Regular Army for Tear and did him some favors afterwards, hence this History of Bull.

All the people mentioned are gone and when I pass on there will be none that will be interested, so I would like to have this book where perhaps it might interest someone—sometime.

I am, Gentlemen,

Respectfully,

ROBERT A. SMITH
430 South Gardner Street
South Bellingham
Washington

Two letters of explanation from Lieutenant Tear addressed to Gen. John C. Smith were with the pictographic record.

FORT RANDALL, D. T.

August 10, 1882

DEAR GENERAL :

Yours of 31st ult., with photographs of yourself and wife recd. Many thanks. Mrs. Smith looks younger than she did 20 years ago—fact—you don't look very old yourself. I may be a little prejudiced in this matter as I am "passing off" as a young man yet.

I have Sitting Bull's description of the paintings, taken down when the pictures were made. Am copying them for you, and will send them next mail. Intended to send them with the book, but I had to send the book to keep it from being stolen. I came near losing it. Some tourists wished to look at it and then borrowed it for a while to show to some friends. I only got it back "by a scratch." They had hidden it with the intention of carrying it off. As soon as I got my hands on it, I put it into the mail.

Bull is very diffident about giving any incidents of his fights with the whites. I have tried to have him give me a detailed description of the Custer fight but he seems rather timid. Once in speaking of the affair he said: "I did not hunt Custer. I thought I had a right to protect my own women and children. If he (Custer) had taken our village he would have killed our women and children. It was a fair fight."

I will try and get him to make a picture of some portion of the fight.

I will try and think of some trinket that would please him as a gift from you—something that will cost but little—I can't think of anything at present.

Am quite well. Have been out in the field a good deal this summer and am quite busy. I have the luck to be alone with the Co. most of the time.

Love to all. Of course you will be elected. If you need my vote I will come home on election day.

Yours truly,
W. TEAR (signed)

FORT RANDALL, D. T.
August 16, 1882

DEAR GENERAL:

I send you inclosed Sitting Bull's interpretation of his paintings recently sent you.

I furnished the book which contains the paintings and from time to time saw him at work on them. These notes were taken down by me, after the paintings were completed, in Sitting Bull's tipi in the same routine as given by himself (thro an interpreter of course) Bull having the picture before him while giving a description of the fight. It was impossible to locate the scenes with any definiteness; "The Land of the Sioux"; "The Land of the Crows" and "a long way from the Missouri" being the usual location given. In talking of his life Bull uses his name instead of the pronoun "I"; that is he speaks in the third person. In these notes you must understand that it is Sitting Bull speaking. Bull made these pictures for me to show his gratitude for blankets and clothing furnished his children last winter before the Government supply of clothing for his band arrived.

I am endeavoring to get him to complete his history up to the present time, and if successful you shall have it.

Bull says he is 43 years old. I think he is nearer 50. These scenes of his life of course comprise his life from the time that he was able to ride a horse and handle a bow. The scars of the wounds he speaks of are visible now.

Regards to your family.

Yours truly,
W. TEAR (Signed)
Lieut. 25th Infantry

GEN. J. C. SMITH

Chicago, Ill.

250 W. Van Buren Street

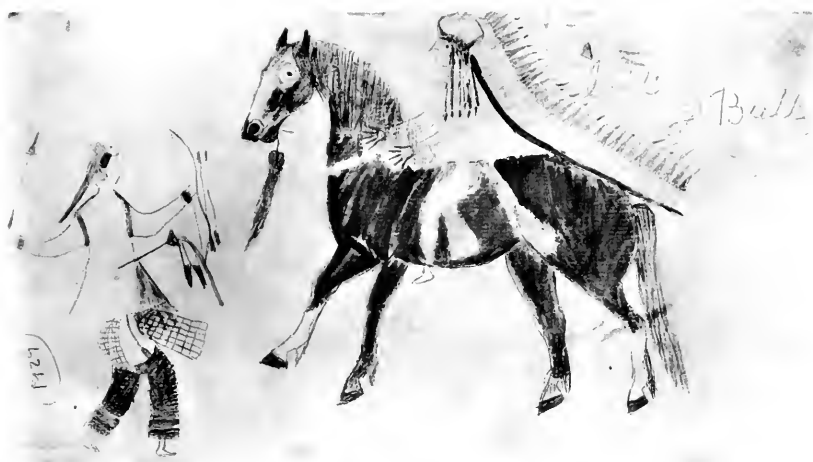
The list of explanations with the picture record are written in the hand of Lieutenant Tear on nine pages of foolscap paper. These explanations are here placed opposite the pictures described, exactly as written.

No. 0

Assinniboine Chief taken prisoner by Sitting Bull in a fight between Sioux and Assinniboinés. 100 Sioux—whole tribe of Assinniboinés engaged—about 27 years ago, when Sitting Bull was about 16 years old—Land of the Sioux. Kept the chief prisoner for while and then gave him the horse he ("Bull") rode and the bonnet he ("Bull") wore in the fight and then sent him to his people with a good heart.

No. 1

Fight with Assinniboinés—140 Sioux—43 Assinniboinés—23 Assinniboinés killed—8 Sioux killed—20 Sioux wounded—"Bull" 18 years old—In land of Sioux. Bull took several prisoners. Didn't kill prisoners. Kept them many days. Gave them ponies and sent them home. Assinniboinés were hunting in Land of the Sioux.



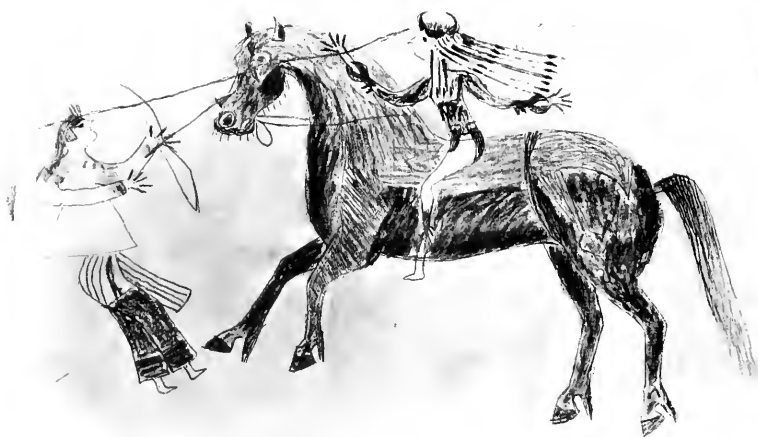
0



1



2



3

No. 2

Scene in same fight.

No. 3

Fight with Assinniboinés. "Bull" 24 years old. 50 Sioux—200 Assinniboinés. No Sioux killed. 5 Assinniboinés killed. "Bull" kills warrior. "Bull" 24 years old.

No. 4

Assiniboiné woman taken prisoner by "Bull" in a fight. "Bull"
16 years old.

No. 5

Same fight. 5 women captured by "Bull."



4



5



6



7

No. 6

Same fight. Woman captured by "Bull." The warrior touches [sic] woman with his lance and she becomes a prisoner. Warrior never strikes a woman in a fight except to save his own life. These women were kept with the Sioux a short time and then sent back to their own people except 3 who married Sioux warriors and remained; one of them here now. No one killed in this fight. Assinniboines passing thro Land of the Sioux.

No. 7

Fight with the Crows. Crow Indian killed by "Bull." 30 Sioux warriors—200 Crows, men, women and children. 14 Crows killed. No Sioux killed. Crows were travelling with their camps. "Bull" 20 years old. On the Little Missouri river, "Crows always fighting the Sioux—tried to make friends with them but they were always doing something bad."—BULL.

No. 8

Fight with Assinniboines. Warrior killed by "Bull." 350 Sioux run upon 10 Assinniboines and killed 2. 1 Sioux killed and 2 wounded. Land of the Sioux, a little above the forks of the Missouri near mouth of Yellow Stone. "Bull" 25 years old.

.

No. 9

Scene in same fight described in No. 7. "Bull" kills Crow Indian.

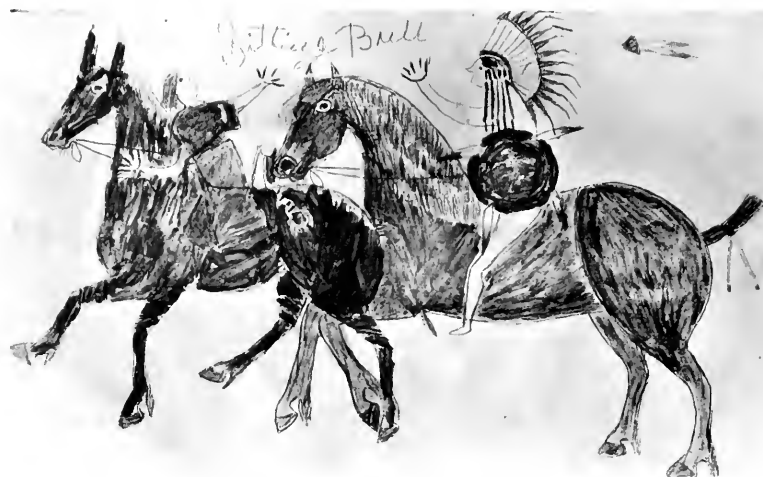
.



8



9



10



11

No. 10

Fight with Crows. "Bull" killed 2 men and captured 2 women. "Bull" 25 years old. Crows were stealing ponies. Let women go home with presents for Crow chiefs to try and make friends.

No. 11

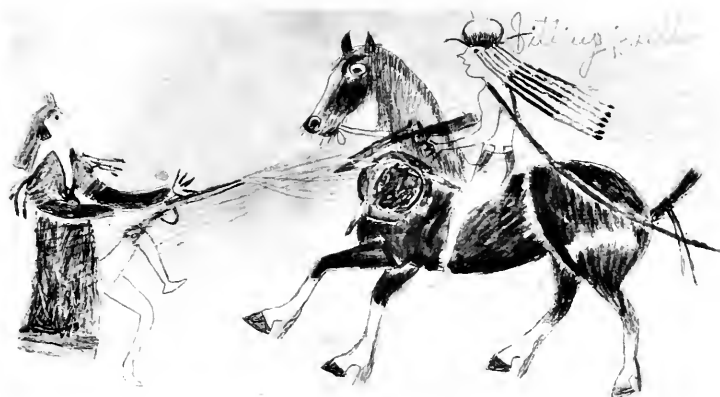
Fight with Crows. 100 Sioux—whole tribe of Crows. Bull killed Crow Chief. 3 Crows killed. 1 Sioux warrior and 1 woman killed. Land of the Sioux—a little above Tongue River. Bull 22 years.

No. 12

Same fight. "Took long time to kill these people. Here is where I got wounded in leg and got off of horse and killed this man. No prisoners in that fight. This is 'Stand and Kill' Crow Chief. Had guns in this fight. The Sioux used to take the Crows prisoners and give them good clothes and feed them up and give them good ponies and then send them back so they could tell a good story of the Sioux to their people." ("Bull's" description of fight.)

No. 13

Fight with Assinniboinés. "Bull" takes 2 prisoners. "Bull" 30 years old. 300 Sioux—20 Assinniboinés—2 Assinniboinés killed—no Sioux killed. On the big fork of the Missouri. "Bull" took one prisoner, "Jumping Bull," home to his (Bull's) tipi (wigwam) gave him his ("Bull's") horse and war bonnet. Jumping Bull's father was a Chief. Jumping Bull is now at Standing Rock (Fort Yates, D. T.) with my people. They call him my son.



12



13



14



15

No. 14

Fight with the Rees. 16 Sioux. 100 Rees. Sioux were fighting and retreating. Sioux turned and chased Rees. This Ree Indian, Chief "Bull Head," fell down dead. "Bull" took him prisoner and he came to life again. This is the only Ree caught in the fight. No Sioux killed. In the land of the Rees. "Bull" sent this prisoner home with presents. Made peace with Rees, and peace with Assinniboinés. "Bull" 33 years old.

No. 15

Fight with Gen. Miles' Scouts and Crow Indians. "Bull" kills "Brave Indian," one of Gen. Miles Scouts. About three years ago—the time Gen. Miles was out after the Sioux near the Queens' land (Canada) "Brave Indian" was away ahead of the soldiers and was following up the Sioux too close. "Bull" turned and killed "Brave Indian." One Cheyenne Indian (scout) also killed. Sioux did not fight soldiers—wanted to get away from soldiers. The scouts and Crows killed 5 Sioux before they got to Canada. Gen. Miles' Scouts seemed to be from every Indian nation. The Sioux run away.

No. 16

Fight with Flat Heads. "Bull" wounded in left arm and side by arrow. "Bull" killed Flat Head. 15 Sioux, young men, went on war path. Flat Heads killed them all. Sioux then went out with 300 warriors. 40 Sioux attacked the camp of the Flat Heads; the main body of Sioux being hid back from the camp; the Flat Heads chased the 40 Sioux back through the main force of Sioux. The Sioux charged and killed 33 Flat Heads. 4 Sioux killed—good many wounded. 7 years ago. Bull 36 years old. Near Muscle Shell river.

No. 17

Crow Indian killed by "Bull." 200 Sioux run upon 7 Crows hunting in Land of the Sioux and killed them all. Crows had guns. Sioux had nothing but bows and lances. Crows were crossing Missouri—(river). A few years ago. ("Bull" gave his age at the time of this fight but my notes are defaced at this point so that I am uncertain as to how old he said he was.—TEAR.)



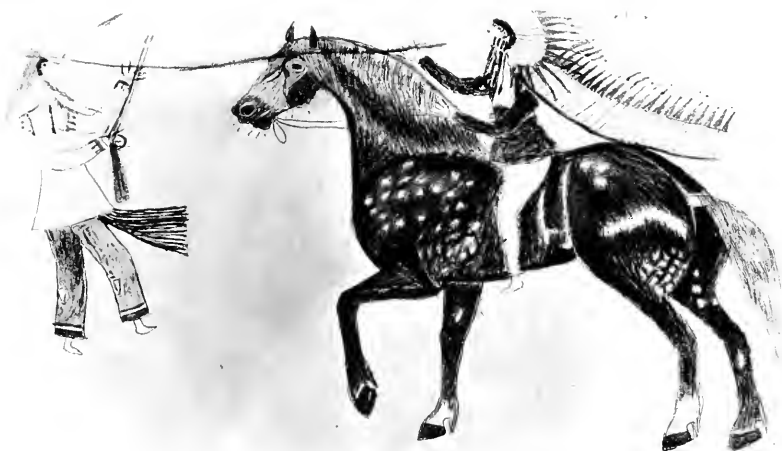
16



17



18



19

No. 18

Fight with Crows. 200 Sioux—whole tribe of Crows. "Bull" kills Crow warrior. 5 Crows killed in the fight. No Sioux killed. "Bull" 33 years old. (Chicken Hawk, skinned and skin stuffed, worn as ornament where picture of bird is seen near Bull's head.)

No. 19

Fight with Crows. 200 Sioux—whole tribe of Crows. "Bull" kills warrior. 7 Crows killed. No Sioux killed. "Bull" dressed in war bonnet trimmed with eagle feather. "Bull" 24 years old. Near mouth of Tongue River.

No. 20

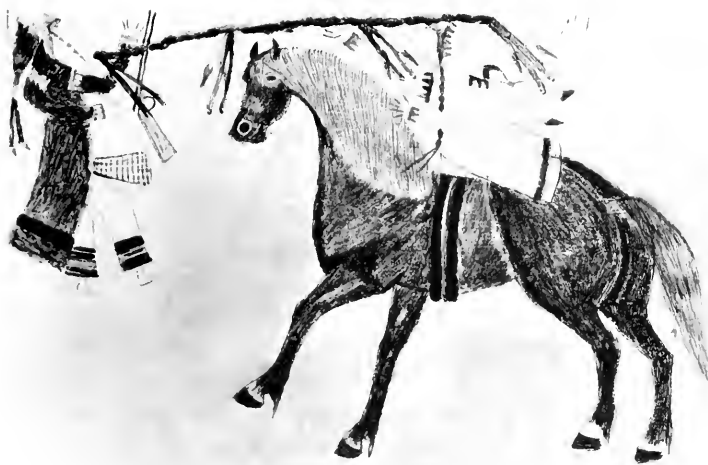
Fight with Assinniboinés. 100 Sioux—60 Assinniboinés. "Bull" kills warrior. 3 Assinniboinés killed. 1 Sioux wounded. Near big fork of the Missouri. "Bull" 29 years old.

No. 21

Fight with Assinniboinés. 320 Sioux attacked big winter camp of Assinniboinés. Bull kills warrior. 5 Assinniboinés killed. No Sioux killed. Did not get in to their (Assinniboinés') camp—there were too many and fought too well. Sioux run off after killing these men.



20



21

III. THE PETTINGER PICTOGRAPHIC RECORD

During the month of February, 1938, a news release appeared concerning the Sitting Bull autobiographies in the Bureau of American Ethnology. The following letter came as a result:

OSWEGO, OREGON

March 7, 1938

SMITHSONIAN INSTITUTION
Washington, D. C.

GENTLEMEN:

My uncle the late Dan'l L. Pratt of Seattle was Post Trader at Fort Randall, Dak. Ter. in 1882, 56 years ago and knew Sitting Bull and his band very well.

Sitting Bull sketched for him 13 pictures of himself on horseback showing him in action against the Crows, Gros Ventres etc.—each one is drawn on paper 10½ by 8½ inches and marked in print—D. L. Pratt, Post Trader, Fort Randall, 188-. The horses are very well drawn—in Indian style—some in colors. These pictures came to me in book form bound in oil cloth. I now have them with the affidavit of Mr. Pratt in a large walnut frame—they are quite impressive.

Hoping this information will be interesting,

I am

Yours truly,

/s/ MRS. G. H. PETTINGER

Oswego, Ore.

The writer communicated at once with Mrs. Pettinger, who very kindly forwarded the pictures to the Bureau of American Ethnology so that they could be included with this publication. They belong to the George Howard Pettinger Collection, which contains several other very interesting Sitting Bull items, including the tomahawk surrendered by Sitting Bull to Lieutenant Ogle on the occasion of Sitting Bull's surrender to the Commanding Officer at Fort Buford, Dakota Territory. The writer wishes here to express his deep appreciation to Mr. Pettinger for making available this interesting addition to the Sitting Bull record.

These pictures, like those of the Smith autobiography, were made at Fort Randall in 1882 and were probably painted from the same paint box, as the shades of the colors used are identical in the two sets. The Pettinger drawings are exactly the same in style but lack the signature. In the Pettinger drawings, Nos. 2 and 5 are unique in that full-face figures are shown. It seems probable that some pictures are missing from the series as originally drawn, for in two instances the descriptive sequence appears to refer to a preceding episode which is not shown.

No. 1

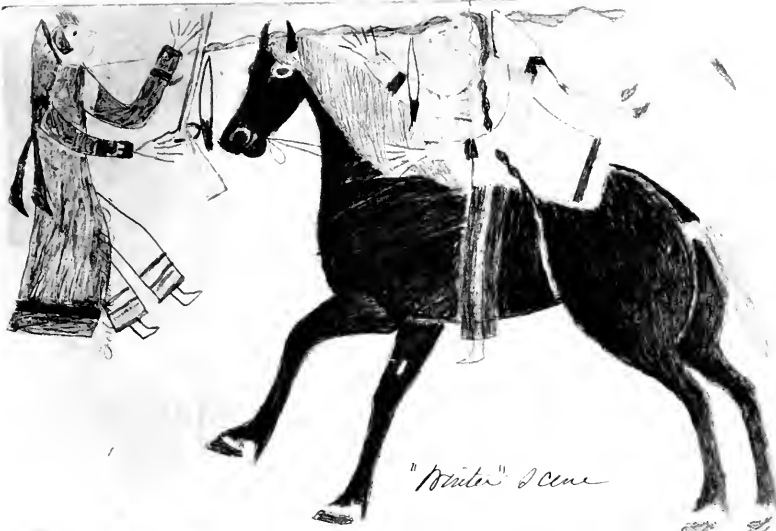
"Winter" scene. Killing a Gros Ventres Indian—100 Sioux on war path killed 3 Gros Ventres whom they found hunting.²⁶

²⁶ This is the same episode as that shown in No. 21 of the Smith autobiography. The horse is blue-black in color. Sitting Bull is wearing black army trousers with a red stripe. His victim wears a green blanket coat.

No. 2

1860. Sitting Bull killing a Crow Indian. One hundred Sioux chased thirty Crows all night. Caught them in the morning and killed them all.²⁷

²⁷ This is probably the fight that took place in the winter of 1869. See Vestal, p. 115.



"Winter" Scene

Killing a Goose. Osage Indian - 1868. Scene in
near Park Killdeer & Goose Osage. Shows way
found hunting.

1

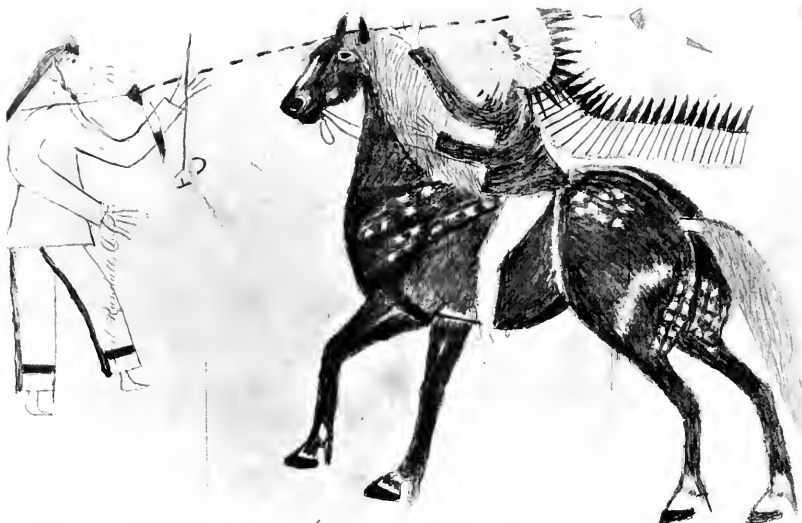


1868

Sitting Bull killing a Crow Indian -
One ^{hundred} days chased they came at night caught them
in the morning and killed them all -

2

2



*Sitting Bull killing a Crow Indian - 40 days
against 7 Crows - Sitting Bull killed 3 Crows
in the fight.*

L PRATT II

3

3



Donna fight

7

4

No. 3

Sitting Bull killing a Crow Indian. 40 Sioux against 7 Crows.
Sitting Bull killed 3 Crows in this fight.

No. 4

Same fight.

No. 5

Sitting Bull killing a Crow Indian.²⁸

²⁸ Sitting Bull is here shown wearing the same costume depicted in No. 2. These two pictures are unique in that in three instances the men pictured are shown in full face instead of profile.

No. 6

Killing a Flathead Indian in a battle.²⁹

²⁹ Sitting Bull is wearing a shirt covered with green spots.



Killing Bull Killing a Crow Indian

5



Killing a Flat Head Indian in a battle before

6

6



*Killing a Flat Head and receiving an arrow
wound in left side*

7



*200 Sioux in a
fight with 50 Chippewas
Yellow River killed one*

"
D. L. PRATT JR.

8

8

No. 7

Killing a Flathead and receiving an arrow wound in left side.³⁰

³⁰ This is the same episode as depicted as No. 16 of the Smith series. This battle with the Flatheads and the particular incident here shown is described by Vestal, p. 125.

No. 8

200 Sioux in a fight with 50 Chippeways. Sitting Bull killed one.³¹

³¹ Sitting Bull is mounted on a yellow horse, black nose and ear tips. His shield is painted blue. In all of the other pictures in which the shield is shown, the color is green.

No. 9

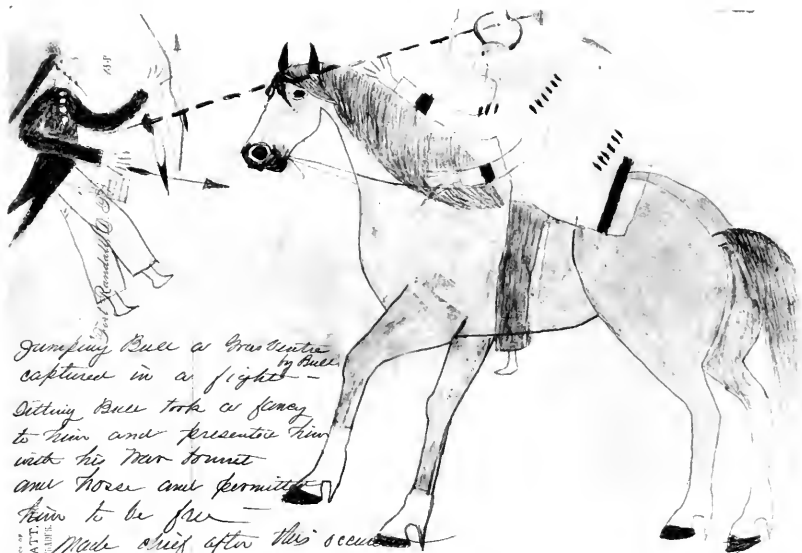
Jumping Bull, a Gros Ventres, captured in a fight by Bull—Sitting Bull took a fancy to him and presented him with his war bonnet and horse and permitted him to be free—made chief after this occurrence.³²

³² This represents the same episode as pictured in No. 13 of the Smith record and No. 5 of the Kimball record.

No. 10

1880. Killing a Crow Indian Scout who belonged to General Miles' command. Sitting Bull wears a war bonnet which once belonged to Crazy Horse.³³

³³ This represents the same episode shown in No. 15 of the Smith record. The horse in each instance is colored a light purple, probably a roan.



*Jumping Bull a Gros Ventre
captured in a fight -
Sitting Bull took a pony
to him and presented him
with his war bonnet
and horse and permitted
him to be free -
Made chief after this occurred*

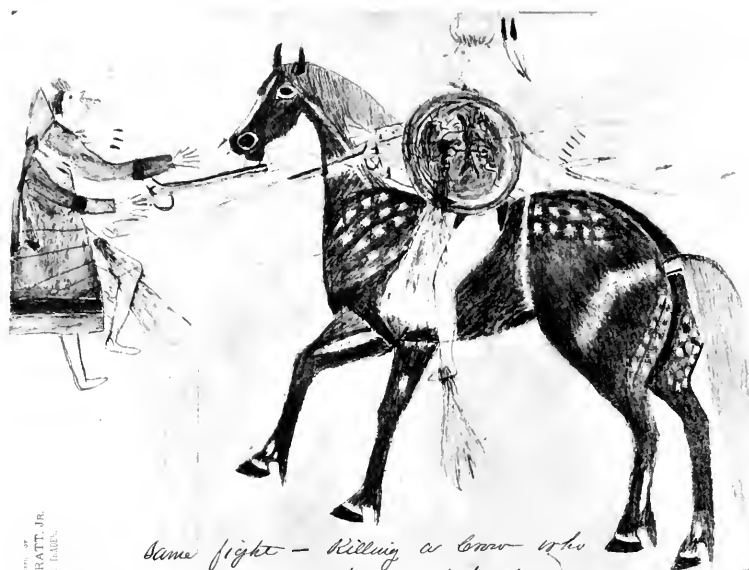
D. L. PRATT, JR.
PEN. TABLE



1880

*Killing a Gros Indian scout who belonged to Gen. Miles
command. Sitting Bull means war bonnet which
was belonged to Crazy Horse*

D. L. PRATT, JR.
PEN. TABLE

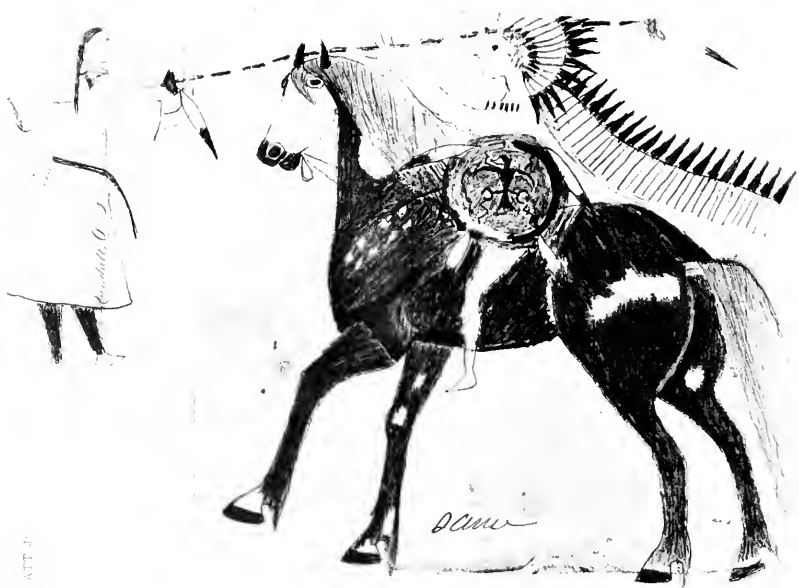


D. L. PRATT, JR.
 NEW HAVEN.

Same fight - Killing a Crow who
 dismounted and fought desperately and wounded Bear
 in two places

11

11



D. L. PRATT, JR.
 NEW HAVEN.

D. L. PRATT, JR.
 NEW HAVEN.

12

12

No. 11

Same fight. Killing a Crow who dismounted and fought desperately and wounded Bull in two places.³⁴

³⁴ This does not refer to the same fight pictured in No. 10. It is the same episode, evidently, as shown in No. 12 of the Smith record and No. 4 of the Kimball record. It was in this encounter that Sitting Bull received the wound in his foot which crippled him for the rest of his life.

No. 12

Same.³⁵

³⁵ This, evidently, does not refer to the same fight as depicted in No. 11. Apparently, it represents the capture of an Assiniboin woman, probably on the occasion shown in Nos. 5 and 6 of the Smith record.

No. 13

Same fight. Killed two.³⁶

³⁶ Sitting Bull is shown wearing a shirt spotted with red. His opponent is wearing a shirt spotted with green. This may represent the fight between the Sioux and the Assiniboines shown in Nos. 1 and 2 of the Smith record.



*Man figh
Killer two*

ARTIST BY
D. L. PRATT, JR.
FISH MARKET
1/2

BIBLIOGRAPHY

JOHNSTON, W. FLETCHER

1891. The Red Record of the Sioux Life of Sitting Bull and History of the War of 1890-91. Edgewood Publishing Company, Philadelphia.

DE BARTHE, JOE

1894. The Life and Adventures of Frank Grouard. Combe Printing Co., St. Joseph, Mo.

MOONEY, JAMES

1897. The Ghost-Dance Religion and the Sioux Outbreak of 1890. 14th Ann. Rep., Bur. Ethnol., pt. 2.

McLAUGHLIN, JAMES

1910. My Friend, the Indian. Houghton Mifflin Co., Boston.

VESTAL, STANLEY

1932. Sitting Bull, Champion of the Sioux. Houghton Mifflin Co., Boston & New York.



SMITHSONIAN MISCELLANEOUS COLLECTIONS

VOLUME 97 NUMBER 6

EVOLUTION OF THE ANNELIDA, ONYCHOPHORA,
AND ARTHROPODA

BY

R. E. SNODGRASS

Bureau of Entomology and Plant Quarantine
U. S. Department of Agriculture



(PUBLICATION 3483)

CITY OF WASHINGTON
PUBLISHED BY THE SMITHSONIAN INSTITUTION
AUGUST 23, 1938

SMITHSONIAN MISCELLANEOUS COLLECTIONS

VOLUME 97, NUMBER 6

EVOLUTION OF THE ANNELIDA, ONYCHOPHORA,
AND ARTHROPODA

BY

R. E. SNODGRASS

Bureau of Entomology and Plant Quarantine
U. S. Department of Agriculture



(PUBLICATION 3483)

CITY OF WASHINGTON
PUBLISHED BY THE SMITHSONIAN INSTITUTION
AUGUST 23, 1938

The Lord Baltimore Press
BALTIMORE, MD., U. S. A.

EVOLUTION OF THE ANNELIDA, ONYCHOPHORA, AND ARTHROPODA

By R. E. SNODGRASS

Bureau of Entomology and Plant Quarantine, U. S. Department of Agriculture

CONTENTS

	PAGE
I. The hypothetical annelid ancestors.....	I
II. The mesoderm and the beginning of metamerism.....	9
III. Development of the annelid nervous system.....	21
IV. The adult annelid.....	26
The teloblastic, or postlarval, somites.....	26
The prostomium and its appendages.....	32
The body and its appendages.....	34
The nervous system.....	39
The eyes	45
The nephridia and the genital ducts.....	45
V. The Onychophora	50
Early stages of development.....	52
The nervous system.....	55
The eyes	62
Later history of the mesoderm and the coelomic sacs.....	62
The somatic musculature.....	64
The segmental appendages.....	67
The respiratory organs.....	70
The circulatory system.....	70
The nephridia	72
The organs of reproduction.....	74
VI. The Arthropoda	76
Early embryonic development.....	80
Primary and secondary somites.....	82
The cephalic segmentation and the development of the brain.....	89
Evolution of the head.....	107
Coelomic organs of adult arthropods.....	126
The genital ducts.....	131
VII. Phylogenetic conclusions	132
References	149

I. THE HYPOTHETICAL ANNELID ANCESTORS

Among the simplest of the metazoic animals that lead an active, free existence is the planula larva of the Coelenterata. The planula develops into a polyp or a medusa because it is a young coelenterate, but, so far as its structure goes, it contains the fundamental building

elements that, with the appropriate hereditary influences, might be fashioned into a flatworm, an annelid, an arthropod, a mollusk, or a vertebrate.

The typical planula is a minute oval or elongate creature (fig. 1 A, C) consisting of an outer layer of ectoderm cells, and an inner mass of endoderm cells. The planula, therefore, represents the gastrula stage of embryonic development, though it may have no enteric cavity and no blastopore. Its motor mechanism is a covering

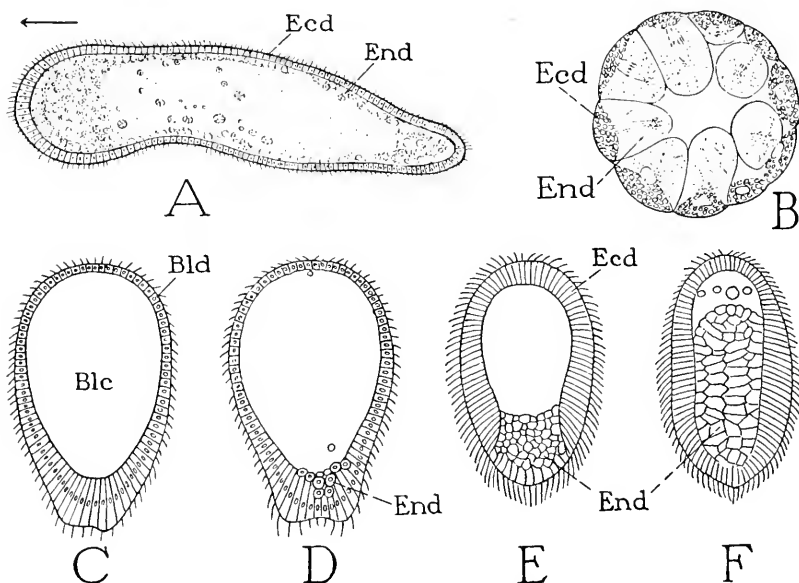


FIG. 1.—The coelenterate planula, and two methods of endoderm formation.

A, planula of *Sympodium corraloides* (from Kowalevsky and Marion, 1883). B, blastula of *Carmarina fungiformis*, showing differentiation of endoderm from ectoderm by delamination of blastoderm cells (from Metschnikoff, 1882). C-F, formation of endoderm by internal proliferation from posterior pole of planula (from Hatschek, 1888, after Claus).

Blc, blastocoele; Bld, blastoderm; Ecd, ectoderm; End, endoderm.

of vibratile cilia. The embryology of the planula is very simple. The cleavage of the coelenterate egg produces a morula, and the morula becomes a blastula. In the succeeding planula stage the inner endodermal cell mass is formed, but it is not certain that gastrulation takes place by simple invagination in any of the coelenterates. With some forms the endoderm arises as an inward migration of scattered cells from the blastoderm; in others the blastomeres divide regularly each into an outer ectoderm cell and an inner endoderm cell (fig. 1 B): but the most common method of endoderm formation is the internal

proliferation of cells from the posterior pole of the blastula (D, E, F), and this last process suggests that it is an embryonic modification of gastrulation by invagination. When, shortly, the planula settles to the bottom of the water and becomes attached preparatory to its metamorphosis into a polyp, a stomach cavity appears in the endoderm, and a mouth cavity breaks through at the free pole.

The development of the planula shows clearly that there is in ontogeny no fixed method for the formation even of so important an organ as the stomach. The effective thing in embryonic development is the inherited organizing property resident in the egg that converts a mass of cells, however formed, into a definite functional structure. The same principle, as we shall see later, applies also to the development of the annelids and the arthropods, for in these animals there is so much apparent irregularity in the formation of the germ layers that attempts to interpret all observed facts in terms of cell genealogy lead only to confusion. Ontogeny and phylogeny, therefore, while they produce the same end results, may follow quite different methods of procedure. In phylogeny we must visualize the successive stages in the evolution of an animal as free-living adult forms, each structurally adapted for performing the functions of an independent animal.

If the coelenterate planula were an adult animal instead of a temporary larval form, or if it had to maintain itself for any considerable length of time, it almost certainly would have a stomach cavity and a mouth. Thus modified, as it is later in its own development, the planula would be an independent, motile gastrula, having a stomach in the form of an open pocket of the blastoderm for the retention of food particles (fig. 2 A). An animal of this simple type of structure, we must suppose, was the actual ancestor of the polyp and medusa forms of the Coelenterata; but equally well it might have been the progenitor of the annelids, and through the latter of the arthropods. Various writers on phylogeny have proposed an origin of the segmented worms direct from a coelenterate polyp, but it should be recognized as a fundamental principle in evolution that a specialized type of animal does not give rise to another specialized type—if two forms are related, they are related through some simple common ancestor. This principle as applied to the coelenterate derivatives is expressed by Ziegler (1898), who says:

It is to be supposed that the higher animals derived from coelenterate stock took their origin not from the highly specialized forms of the Coelenterata, such as the anthozoans and ctenophores, but from a planula-like or gastrula-like ancestral form of the coelenterates.

The theoretical planulalike gastrula postulated above as the common ancestor of the Coelenterata and the Annelida (fig. 2A) presumably swam habitually in one direction by means of a covering of cilia, and the mouth, or blastopore, was at the posterior pole where food particles might be swept into the stomach with the eddy of currents converging to the rear.

In the ontogenetic development of the annelids, gastrulation generally takes place by epiboly, which is the overgrowth of the endoderm by the ectoderm, and the primary open blastopore is at the posterior pole of the embryo. There is no reason why this ontogenetic stage should not represent an early phylogenetic stage, and one identical with the gastrula ancestor of the Coelenterata (fig. 2 A). With the further development of the annelid embryo, however, the blastopore elongates forward on the ventral surface of the gastrula (fig. 2 F) until its anterior end comes to be near the anterior pole (G); but, at the same time, the lips of the blastopore grow together from behind forward, leaving finally only the anterior end open into the archenteron, and this opening is the primitive mouth (H, *Mth*). Secondly, an anal aperture (*An*) is formed later at the original posterior end of the blastopore on the caudal extremity of the embryo. The endodermal archenteron of the annelid thus becomes a simple alimentary canal having the oral aperture located *ventrally near the anterior end of the body*, and the anal aperture situated *terminally at the posterior end*.

If we visualize the change in the position of the blastopore as an event in the phylogenetic history of the annelids, we must see a correlated change in the habits of the animal. The actively swimming gastrula (fig. 2 A) in its search for food, we may suppose, took to brushing over the surfaces of stones or aquatic plants (B), where food particles were more numerous and more easily obtained. For this manner of feeding, a ventrally placed blastopore would be a distinct advantage, or, even more efficient, a blastopore drawn out lengthwise on the under surface (C). With a form thus modified in habits and structure, there may easily have developed a creeping habit, and an adaptation of the ventral cilia for progression on solid surfaces (D). Finally, then, came a more complete adaptation to feeding on a subsurface, resulting in an elongate flattened body, and the establishment of an alimentary canal with a ventral mouth and a terminal anus (E) produced by the closure of the intermediate part of the blastoporic slit.

A creeping mode of locomotion may be subserved entirely by a ciliary coating of the body wall, as is shown in the Platyhelminthes,

but a creeping animal encounters irregularities and obstructions. A provision for body movements, therefore, becomes an advantageous adjunct to the motor mechanism, and such movements can be produced only by an internal muscular system. Hence, the next stage in evolution, recorded in both the flat worms and the annelids, was

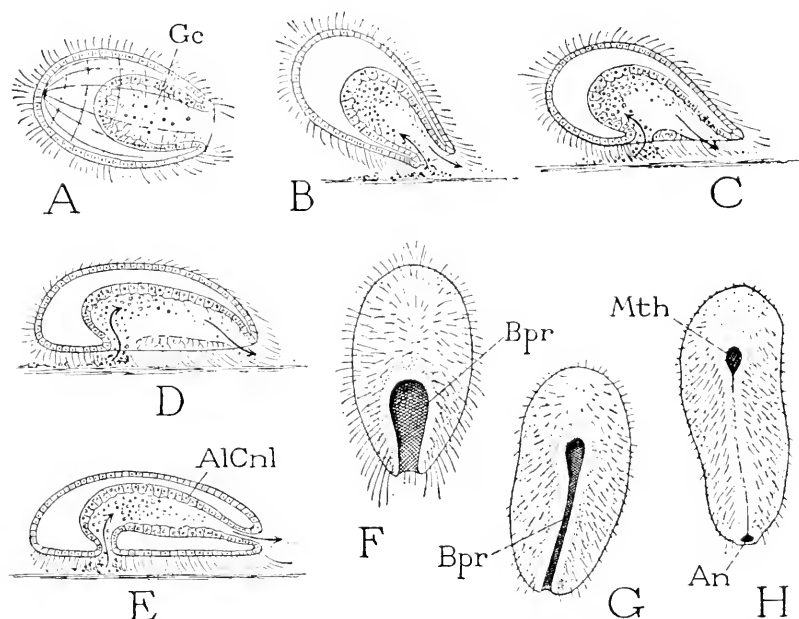


FIG. 2.—Hypothetical evolution of a swimming planulalike creature with an open gastrocoele into a creeping wormlike animal with a simple alimentary canal, a subapical ventral mouth, and a terminal anus.

A, primitive swimming form with posterior blastopore. B, the same having acquired the habit of sweeping up food particles from a solid surface. C, blastopore elongated forward on surface of contact to accommodate the feeding habit. D, the same more fully adapted to subsurface feeding. E, final development of alimentary canal, with ventral mouth and terminal anus, formed by closure of intermediate part of blastopore, creeping habit fully established. F-H, three stages of elongation and closure of the blastopore, ventral view.

AlCnl, alimentary canal; *An*, anus; *Bpr*, blastopore; *Gc*, gastrocoele, or archenteron; *Mth*, mouth.

the development of contractile tissue that conferred the power of diversified adjustive movements on the body itself. Muscles, however, are not generally automatically active, as are cilia, and hence the development of muscle tissue is usually accompanied by the development of a mechanism for its activation. Furthermore, since a muscular system is a provision for adjustment to external conditions, the source of its stimulus must come from the environment. The sponges are said to have a primitive contractile tissue that is

stimulated directly by environmental changes; in all other animals there is intimately associated with the contractile muscle tissue a specifically receptive and conductive nerve tissue, through which environmental stimuli become effective on the muscles. Finally, the high metabolic rate of muscular activity creates the need of special excretory organs for the removal of waste products from the body.

The genesis of contractile and conductive tissues, and their integration into a neuromuscular system are best seen in the Coelenterata. Contractility, being a common property of protoplasm, may become localized and specially developed in a particular part of any cell of the body in a primitive animal. In the coelenterates fingerlike muscle processes are produced from the inner ends of cells in both the ectodermal and the endodermal epithelium, those of the ectoderm (fig. 3, *mp*) taking a longitudinal course, those of the endoderm a

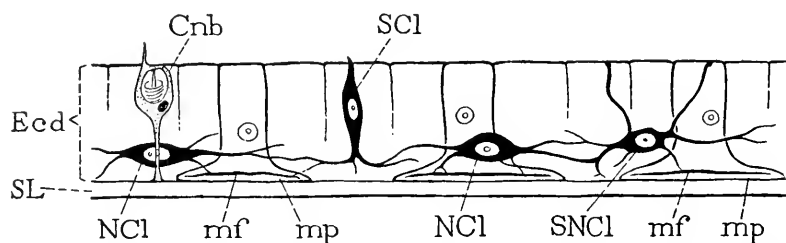


FIG. 3.—Diagram of the ectodermal neural and muscular elements of *Hydra*. (From Curtis and Guthrie, 1927.)

Cnb, cnidoblast; *Ecd*, ectoderm; *mf*, muscle fiber; *mp*, muscle process of epithelial cell; *NCl*, neural cell; *SNCl*, neurosensory cell; *SCl*, sensory cell; *SL*, supporting lamella.

transversely circular course. Fibrils of contractile tissue (*mf*) become differentiated in these processes. In the hydra, the body of the muscle cell remains as a part of the epithelial layer, but in some of the other coelenterates the entire cell may be withdrawn beneath the surface and converted into a muscle fiber. A primitive nerve cell is an epithelial cell in which the common protoplasmic properties of irritability and conductivity are specially developed both in the cell body and in branching processes given off from the latter, but the nerve cells become differentiated into superficial receptive cells and deeper-lying conductive cells. In the hydra the receptive cells (fig. 3, *SCl*) and the sensory cells (*SNCl*) contained in the ectoderm have connections, on the one hand, with the surface of the body, and, on the other, send branches to the strictly neural cells (*NCl*), which are distributed through the inner parts of the ectoderm, and in turn send branches to the muscle processes of the muscle cells. The endo-

derm of the coelenterates, though its cells have numerous muscle processes, contains relatively few sensory and neural cells, and fibrous branches of these cells are but little developed.

The polychaete annelid larva of the trochophore type (fig. 8) has a muscular system of which the elements appear to be quite analogous to the ectodermal muscles of the coelenterates, though the system itself is carried to a higher degree of development. Furthermore, the larval muscles are parts of a neuromuscular system, since generally they follow the inner surfaces of nerve tracts in the ectoderm. The muscle fibers are formed from cells derived directly from the larval ectoderm, along with numerous small undifferentiated cells that constitute a loose layer of mesenchyme distributed through the haemocoel. The fibers are arranged principally in longitudinal and circular tracts, though some of them extend from the body wall to the alimentary canal. The endoderm of the larva does not produce directly either muscular or neural cells. The nervous system of the polychaete larva, when best developed, consists of longitudinal and circular strands of ectodermal nerve cells and fibers following the muscle tracts, and of ganglionic groups of nerve cells developed particularly in connection with sensory organs on the preoral part of the body. The larval elaboration of the neuromuscular system is largely a temporary adaptation to the specialized form and habits of the trochophore, for most of it is lost when the larva undergoes its metamorphosis into the definitive worm form; but the preoral part of the larval nervous system forms the brain of the adult, and some of the larval muscle fibers are taken over into the definitive muscular system.

If now we endow our hypothetical annelid ancestor (fig. 2 E) with a primitive neuromuscular system derived from the ectoderm, and provide it with a pair of primitive nephridia, it will have reached an evolutionary stage entirely comparable in structure with that of an annelid in the ontogenetic stage of the young polychaete larva. The usual trochopore larva of the Polychaeta (fig. 4 A), however, leads a purely pelagic life; it floats upright in the water and swims by means of bands of cilia that encircle the body. Its radial and circular neuromuscular system appears to be entirely adapted to its upright position, and many zoologists have regarded the trochophore as the ancestral form of the annelids as well as of various other invertebrates. The lateral position of the mouth, however, just below the principal circle of cilia (*Mth*), gives us good reason for suspecting that the shape of the trochophore and the position assumed in the water are secondary adaptations to a brief swimming existence;

in fact, the later horizontal development of the worm form along the vertical axis of the larva shows clearly that the trochophoral position is one quite out of harmony with the general organization of a worm.

The trochophore, therefore, is to be regarded as a temporary, specialized larval form in polychaete ontogeny, adapted to a free pelagic life for the purpose of disseminating the individuals of its species. The metamorphic alterations that it undergoes at its transformation to the worm are changes of a nature that could not have been a part of the phylogenetic evolution of any animal. On the

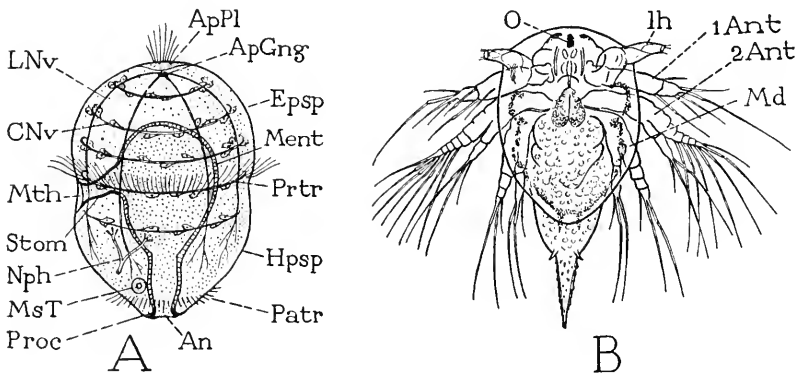


FIG. 4.—The polychaete trochophore and the crustacean nauplius, two specialized larval forms of an early ontogenetic stage, having, therefore, primitive characters, but no phylogenetic significance in their shape or general structure.

A, typical structure of a trochophore, diagrammatic. B, nauplius of a cirriped, *Alcippe lampas* Hancock, dorsal surface (from Kühnert, 1935).

An, anus; 1Ant, first antenna; 2Ant, second antenna; ApGng, apical ganglion; ApPl, apical plate; CNV, circular nerve; Epsp, episphere; Hpsp, hyposphere; lh, lateral horn; LNV, longitudinal (radial) nerve; Md, mandible; Ment, mesenteron; MsT, mesodermal teloblast; Mth, mouth; Nph, nephridium; O, naupliar ocellus; Patr, paratroch; Proc, proctodaeum; Prtr, prototroch; Stom, stomodaeum.

other hand, inasmuch as the trochophore is an early ontogenetic stage, its general organization is primitive, and is repeated in the ontogenetic development of many other invertebrates besides the annelids. It should be noted, furthermore, that the trochophore is not a universal larval form even among the annelids, for most of the archannelids, some of the polychaetes, and all the oligochaetes have a direct development, in which either there is no suggestion of the trochophore form, or a remnant of it is preserved from ancestors that had a typical swimming larva.

The presence of a mesoblastic muscle system and of a mesenchyme, or parenchymatous layer between the ectoderm and the endoderm, gives the annelid larva, or the platyhelminth adult, the status of a triploblastic animal; but the middle layer is here only an elaboration of elements present also in the so-called diploblastic coelenterates. The young annelid larva, however, is endowed from its parents with hereditary influences that will mold its growing tissues into structures never attained by the coelenterates or flat worms. Particularly affected are two individualized groups of mesoblast cells, which, though they may be set apart in the platyhelminths, will give rise in the annelids to special bands of mesoblastic tissue, known as the *mesoderm*. Within the mesoderm will be formed a new body cavity, the *coelom*, and from the walls of the latter will be produced a new muscular system, a more efficient excretory system, a circulatory system, and various tissues of special functions, to all of which is added an extension and elaboration of the nervous system. With the formation of the mesodermal cavities the triploblastic annelid larva becomes a coelomate animal, but, shortly before the appearance of the coelom, there takes place a segmentation of the body affecting the ectoderm and the mesoderm, so that the young annelid worm is almost at once a segmented and a coelomate animal.

II. THE MESODERM AND THE BEGINNING OF METAMERISM

In the ontogeny of the articulate animals, the formation of the coelomic cavities in the mesoderm is so closely associated with the appearance of body segmentation as to give the impression that the two are intimately related developmental processes, and since the segmentation of the mesoderm is usually more conspicuous than the segmentation of the body, embryologists often describe metamerism in terms of mesoderm segmentation, as if the formation of "mesoderm somites" were equivalent to body segmentation. Closer attention recently given to the sequence of events in the development of the Polychaeta, however, shows that metamerism begins in the ectoderm and the primary ectodermal musculature, and that it secondarily effects a division of the coelomic mesoblast into segmental sections. Subsequently, the coelomic cavities are formed in the segmented mesoderm. That coelomic sacs do not determine metamerism is shown also by the formation of paired coelomic cavities in the preoral cephalic mesoderm of the Onychophora and Arthropoda, in which there is no corresponding external segmentation.

Metamerism, therefore, probably took its origin in a subdivision of the primary somatic musculature into successive sections (myo-

tomes) to give greater efficiency to body movement. The segmentation of the ectoderm and the mesoderm then followed as a result of the segmentation of the muscular system. The primitive coelomic cavities were probably spaces formed in the mesoderm for the accumulation of waste products in the body fluid, to be discharged through primitive nephridial tubules. The coelomic mesoblast, however, formed also a secondary musculature that reinforced the primary musculature, and which, in the higher arthropods, has completely replaced the latter. Evidence that such has been the course of evolution in the Articulata will be shown in the following discussion of the early stages in annelid ontogeny; but there still remains the question as to the origin and nature of the primitive mesoderm, which antedates metamerism.

A study of the growth and differentiation of the annelid mesoderm takes us into the later part of larval development, but to obtain light on the origin of the middle germ layer we must go back to an earlier ontogenetic stage. During cleavage of the annelid egg most of the yolk remains consistently in the blastomeres situated on the vegetative surface of the blastula (fig. 5 A), with the result that, in the 64-cell stage, there are 8 large, yolk-filled blastomeres at the posterior pole (B). These cells are designated by embryologists *4A*, *4B*, *4C*, *4D*, and *4a*, *4b*, *4c*, *4d*, since they comprise the so-called macromeres of the fourth generation and the fourth quartet of micromeres. All of them at this stage would appear to be endodermal, and at the time of gastrulation they all become internal, owing to their overgrowth by the ectoderm. Seven of them, in fact, give rise to purely endodermal progeny, but the *4d* cell will form in most cases both endoderm and mesoderm. The first cleavage of *4d* produces two bilaterally symmetrical cells, *4d*¹ and *4d*² (C), and these cells, in their immediately following divisions, give rise to a few very small cells (*D*, *end*), usually regarded as endoderm cells, and a pair of large cells (*MsT*) that are destined to produce the coelomic mesoblast, and hence constitute the *mesodermal teloblasts*. (It is perhaps possible that the small "endoderm" cells of this generation are the primary germ cells.)

The common occurrence in the annelids of mesodermal teloblasts derived from cells closely associated with the endoderm has given rise to the idea that the coelomic mesoblast is of endodermal origin, and for this reason it is often called the "endodermal mesoblast" to distinguish it from the larval mesoblast, which is derived from the ectoderm. In most animals the mesoderm is, one way or another, associated in its origin with the endoderm, but among the annelids there are many cases where its endodermal connection is not evident.

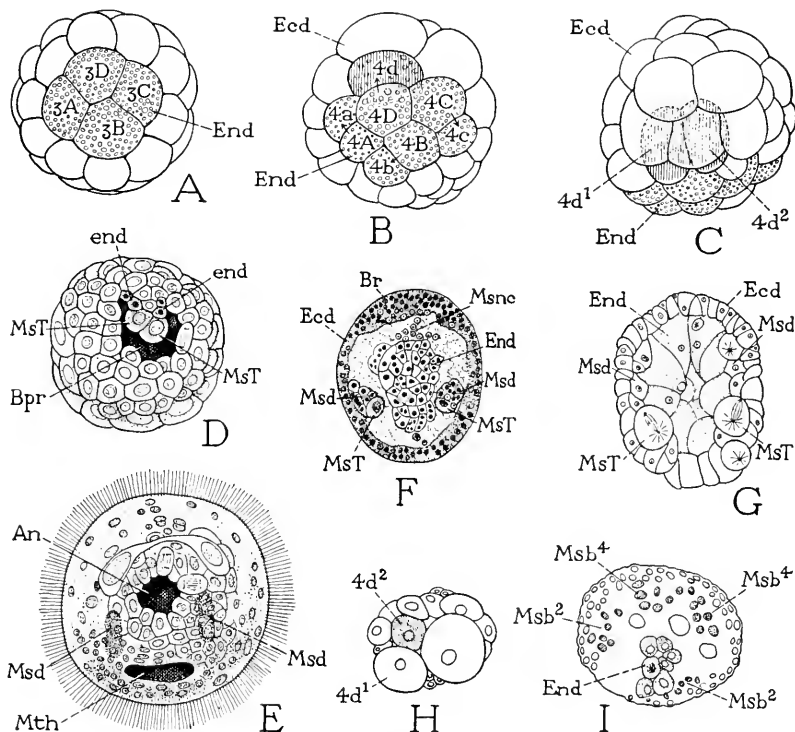


FIG. 5.—Late cleavage stages and mesoderm formation in Annelida and Platyhelminthes.

A, diagram of posterior pole of annelid blastula showing four yolk-filled "macromeres" of third generation. B, posterior pole of blastula of *Arenicola cristata* Stimpson after next cleavage forming fourth quartet of "micromeres," showing differentiation of $4d$ blastomere (adapted from Child, 1900). C, same, after cleavage of $4d$ into $4d^1$ and $4d^2$ (adapted from Child, 1900). D, blastula of *Podarke obscura* Ehlers, showing mesodermal teloblasts (MsT) derived from blastomeres $4d^1$ and $4d^2$ (C) after separation of small endoderm cells (from Treadwell, 1901). E, posteroventral view of 40-hour embryo of *Podarke obscura* with mouth and anus, showing position of mesoderm bands (Msd) in body (from Treadwell, 1901). F, optical frontal section of embryo of *Capitella capitata* Fabr., showing mesodermal teloblasts and rudiments of mesoderm bands (from Eisig, 1899). G, optical section of embryo of *Dinophilus* sp., with mesoderm bands (Msd) extending forward from teloblasts (from Nelson, 1904). H, optical section of blastula of *Planocera inquilina* Wheeler (Polychladia) from right side just after division of $4d$, producing $4d^1$ that will form endoderm, and $4d^2$ that will form mesoblast (from Surface, 1907). I, same, later stage seen from posterior pole, showing mesoblast (Msb^1) derived from $4d^2$, and mesoblast (Msb^2) derived from second quartet of ectodermal blastomeres (from Surface, 1907).

$3A-3D$, $4A-4D$, "macromeres" of third and fourth generations; $4a-4d$, "micromeres" of fourth quartet; *An*, anus; *Bpr*, blastopore; *Br*, brain; $4d^1$, $4d^2$, daughter cells of $4d$ blastomere; *Ecd*, ectoderm; *End*, endoderm; *end*, endoderm derived from $4d^1$ and $4d^2$ blastomeres; Msb^2 , mesoblast derived from second quartet of micromeres; Msb^4 , mesoblast derived from $4d$ cell of fourth quartet; *Msd*, mesoderm; *Msn*, mesenchyme; *MsT*, mesodermal teloblast; *Mth*, mouth.

It is claimed by both Kleinenberg (1886) and E. Meyer (1901), for example, that in the larva of *Lopadorhynchus* the mesoderm arises from the ectoderm, and in *Capitella*, according to Eisig (1899), the coelomic mesoblast is produced from blastomeres other than 4d. Furthermore, the mesoderm of the postlarval somites is said by Iwanoff (1928) to be formed in many polychaetes directly from the ectoderm, and the same is probably true in cases of regeneration. The mesoderm of certain other coelomate invertebrates also may have no genetic relation to the endoderm, as in the gastropod *Paludina*, in which the embryonic mesoblast that gives rise to the usual mesodermal organs is generated directly from cells of the ventral ectoderm (see Dautert, 1929).

During larval life, or at the transformation of the larva to the worm, the annelid mesodermal teloblasts, however formed, proliferate within the haemocoel two masses of mesoderm cells (fig. 5 E, F, G, *Msd*), which eventually take the form of ventrolateral bands extending forward at least as far as the sides of the mouth (fig. 6 F). These primary mesoderm bands are solid cell masses; they are never observed at this early stage to contain cavities, and there is no evidence from annelid embryology to suggest that they represent phylogenetically a pair of open pouches. Later, with body segmentation, the bands are broken up into solid segmental blocks (G), and finally the blocks are excavated by coelomic cavities (H). The nature of the mesoderm and the primitive function of the coelomic cavities can be better discussed after we have examined the known facts concerning the beginning of metamerism, but it should be noted here that the formation of the mesoderm bands precedes body segmentation.

Metamerism in the polychaete larva becomes first evident as a subdivision of the body region between the mouth and the pygidium into a small number of somites (fig. 7 A, I, II, III). There is ample reason to believe, as Iwanoff (1928) claims, that the formation of these *primary somites*, or *larval segments* of ontogeny, represents the beginning of metamerism in phylogeny, and, as we shall see, the same phenomenon of direct segmentation in the body of the embryo or young larva recurs in various arthropods. The primary somites are thus to be distinguished from the *secondary somites* later added by teloblastic growth in a subterminal generative zone, and which will constitute the major part of the adult animal. The larval somites of the Polychaeta, Iwanoff shows, are formed approximately simultaneously in contrast with the successive, individual generation of the teloblastic somites. E. Meyer (1901) observes that in *Lopadorhynchus* metamerism takes place so rapidly as to give the impres-

sion that a relatively large number of somites are formed all at once, but Sokolow (1911) says that in *Ctenodrilus* the intermediate somites or the more anterior ones are first differentiated and the series then completed anteriorly and posteriorly. Segmentation may be delayed until the beginning of metamorphosis, as in *Polygordius*, or it may take place while the larva is still in the swimming trochophore stage.

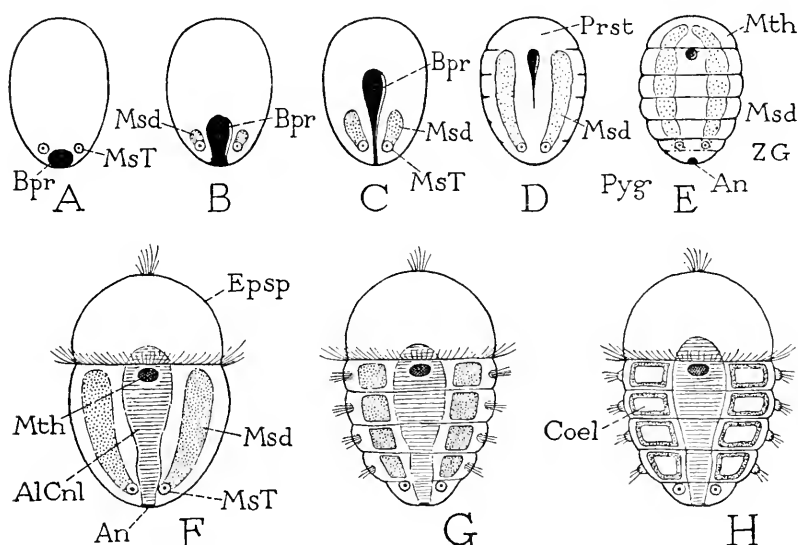


FIG. 6.—Transformation of the annelid blastopore, primary segmentation of the body, growth and segmentation of the mesoderm bands, and formation of the coelomic sacs, diagrammatic.

A, blastopore and mesodermal teloblasts at posterior pole of embryo. B, blastopore elongating forward on ventral surface; rudiments of mesoderm generated from teloblasts. C, blastopore still more elongate, closing posteriorly; mesoderm growing forward. D, blastopore closed posteriorly; mesoderm bands extended to prostomium. E, blastopore obliterated except for mouth opening at anterior end; anus formed secondarily at posterior end; mesoderm segmented following metamorphosis of body, and extended into prostomium. F, polychaete trochophore before segmentation. G, same after segmentation, mesoderm cut into solid segmental blocks. H, same, mesoderm blocks excavated by coelomic cavities.

AlCnl, alimentary canal; *An*, anus; *Bpr*, blastopore; *Coel*, coelomic cavity; *Epsp*, episphere; *Msd*, mesoderm; *MsT*, mesodermal teloblast; *Mth*, mouth; *Prst*, prostomium; *Pyg*, pygidium; *ZG*, zone of growth.

In *Polynoë*, as described by Hacker (1895), seven somites are first marked out in the body of the trochophore, which is transformed while still active into a swimming "nectochaete" larva with seven segments and corresponding chaeta-bearing parapodia. The number of larval somites is always small, three or four being usual (fig. 7 A, B, C), the maximum not more than 13. Completion of larval metamorphosis is followed by a pause in development.

Observations on the beginning of embryonic segmentation in the annelids differ somewhat as to whether the intersegmental divisions appear first in the ectoderm or in the mesoderm, but most students of annelid development find either that the ectoderm and the meso-

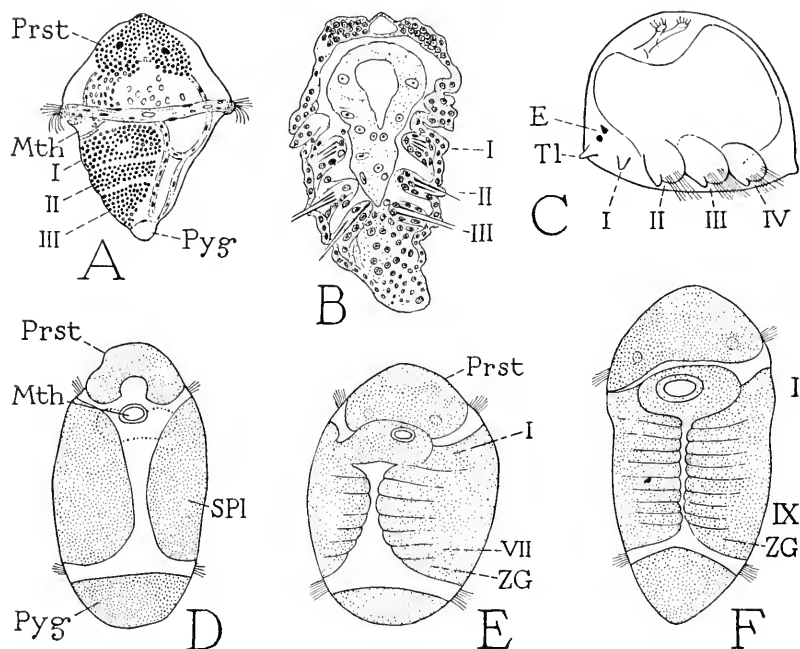


FIG. 7.—Examples of primary segmentation in polychaete larvae.

A, *Eupomatus uncinatus*, trochophore showing primary segmentation of the mesoderm (from Iwanoff, 1928). B, same, later larval stage, horizontal section showing development of chaetal sacs in primary somites, and extension of posterior part of body (from Iwanoff, 1928). C, *Platynereis dumerilii* Aud. & Milne-Edw., nereidogen larva just out of egg, with four primary somites (from Hempelmann, 1911). D, *Capitella capitata* Fabr., embryo before segmentation, ventral view (from Eisig, 1899). E, same, embryo with seven somites and zone of growth formed directly in primary body region (from Eisig, 1899). F, same, later stage with two additional somites formed from zone of growth (from Eisig, 1899).

E, eye; I-IX, somites; Mth, mouth; Prst, prostomium; Pyg, pygidium; SPL, somatic plate; Tl, tentacle; ZG, zone of growth.

derm are segmented at the same time, or that the first signs of metamerism are to be seen in the ectoderm.

In the development of the polychaete *Capitella*, according to Eisig (1899), on the sixth day after fertilization of the egg, the cells of the ventral somatic plates of the larva (fig. 7 D, SPL) become arranged in transverse rows, and on the sixth day seven or eight somites are already demarked by transverse lines in the ectoderm of the larval

body region between the mouth and the pygidium (E). On the same day, however, the mesodermal bands also become divided into segmental sections. At first the ectodermal and mesodermal somites of *Capitella* do not entirely correspond, there being several supernumerary mesodermal divisions in the mouth region, but by the twelfth or thirteenth day the larva has 13 somites with coincident limits in both the ectoderm and the mesoderm.

The segmentation of the mesoderm bands as described by E. Meyer (1901) in *Psymobranchus*, *Polygordius*, and *Lopadorhynchus* appears to be determined by elements of the mesenchymatic primary mesoblast in the form of spindle-shaped cells that penetrate into the mesoderm bands at the intersegmental lines and cut the bands into a series of segmental sections. From the penetrating mesenchyme cells are later formed, according to Meyer, the muscles of the intersegmental dissepiments. Similarly in the Serpulidae and Spionidae the larval segmentation is said by Iwanoff (1928) to be secondarily imposed upon the mesoderm bands by metamerism in other parts of the body, as by the ectodermal segmentation, the ingrowth of the chaetal sacs (fig. 7 B), the penetration into the mesoderm of mesenchymatous muscle elements, or by the segmental formation of blood lacunae in the general mesoderm mass.

The primary larval segments are seldom as fully developed in the adult worm as are the teloblastic segments, and both the segment limits and the differentiation of ganglia on the nerve cords may remain obscure. In the Spionidae, Iwanoff (1928) says, the trochophoral mesoderm is very weakly developed, the dissepiments are only imperfectly formed, often absent, and in some species a segmentation of the mesoderm in the primary segments is absent even in the adult. Chlorogogen cells are not developed in the coelomic walls of the larval segments, and in these segments *germ cells are never present*.

As a result of body metamerism, the mesoderm bands are divided each into a series of segmental sections, and these sections, as the bands themselves, are at first solid blocks of cells (fig. 6 G). Later the coelomic cavities appear as cleavage spaces within the cell blocks (H). Hence, just as there is no evidence that the primary mesoderm bands represent primitive sacs, so there is no evidence from ontogeny that the coelomic cavities of the annelids took their origin as a series of separate mesodermal pouches. The facts of development suggest only that the primitive mesoderm bands were continuous tracts of cells, and that the formation of cavities within them was a secondary process, subsequent to segmentation.

With the formation of the coelomic cavities in the mesoderm, the young annelid becomes a coelomate animal. Before the appearance

of the coelom, however, it might pass for the ancestor of a flatworm, for even in the Platyhelminthes there is a teloblastic proliferation of cells that appear to correspond with the mesoderm cells of the annelids, though the cells thus produced soon disperse and become a part of the parenchyma. It is in the development and elaboration of the mesoderm, or teloblastic mesoblast, therefore, that the Coelomata depart from the Platyhelminthes. Segmentation is a feature superimposed upon the mesoderm in the Annelida as a result of body metamerism, in which apparently the ingrowth of the septal muscles plays an important part.

The mesoderm of the adult annelid or arthropod gives rise to a large variety of tissues and organs, but most of the specialized derivatives of the mesoderm are formed in the secondary segments of the adult animal. The principal products of the primary mesoderm are muscle and connective tissues, and an epithelial lining of the coelomic cavities.

According to E. Meyer (1901), the mesodermal myoblasts of the polychaete larva are not recognizable as such until the mesoderm bands have become broken up into segmental sections, and the transformation of the myoblasts into functional muscle fibers is not evident until after the appearance of the coelomic cavities. The myoblasts of each mesodermal segment, Meyer says, consist of four large cells on each side, two dorsal and two ventral, lying along the lines of the larval longitudinal muscles of mesenchymatic origin already present. The mesoderm fibers finally replace the mesenchyme fibers and become the definitive longitudinal muscles of the worm. The coelomic myoblasts, Meyer shows, are true epithelial muscle cells that form muscle processes from their outer surfaces, while the plasmatic bodies of the cells retain their places for some time in the coelomic walls. The parts of the coelomic walls not involved in muscle formation become thinner, and finally transform into typical peritoneal epithelium.

The important part that the mesoderm plays in the development of the coelomate animals is entirely clear; but what the mesoderm becomes in the course of evolution does not explain what it was in its beginning. Most of the theories that have been proposed to account for the primitive mesoderm, it will be found, are attempts to explain the functional nature of the coelomic sacs rather than the origin of the mesoderm itself.

The theory most widely accepted at one time as to the origin of the mesoderm is the *enterocoele theory* (Hertwigs, 1882, Sedgwick, 1884), by which the coelomic sacs are explained as diverticula of the archenteron. In some animals the coelomic sacs are thus formed in

the embryo, and the enterocoele theory has some plausibility as a wide generalization, considering the very common early association of the coelomic mesoderm rudiments with the endoderm; but, as applied to the annelids and arthropods, the theory must entirely discard the direct evidence from embryology that the mesoderm first appears as solid proliferations of cells, which only in a purely hypothetical manner could be interpreted as representing pouches of the archenteron. The only known case of the formation of the mesoderm from enteric pouches that might be referred to the articulates occurs in the Tardigrada (see Marcus, 1929), but there is much uncertainty concerning the relationships of the tardigrades.

A second mesoderm theory is the *gonocoele theory*, based on the almost universal association of the germ cells with the coelomic mesoderm in the coelomate animals. Hatschek (1877, 1894) believed that the mesodermal teloblasts of the annelid larva are themselves germ cells, and Rabl (1879, 1889) adopted this view. The gonocoele theory of the origin of the coelomic sacs, however, was principally elaborated by E. Meyer (1891, 1901). Meyer contended that the primitive coelomic sacs were muscular pouches, from the epithelial walls of which the germ cells are generated, and that, as these gonadal sacs expanded to increase the reproductive function, they finally preempted the haemocoele, and their muscles were transferred to the body wall. The gonocoele theory loses much of its support now that the old belief that the germ cells are direct products of the coelomic epithelium is no longer tenable, and, moreover, it entirely breaks down in view of the fact that the primary larval somites of the annelids do not contain germ cells. In the primitive annelids, as will be shown later, the germ cells probably were located in the zone of undifferentiated tissue behind the last primary somite. If so, the reproductive function had nothing to do with the origin of the mesoderm or the formation of the coelomic sacs.

A third theory, concerned principally with the function of the coelomic sacs, is the *nephrocoele theory* (Ziegler, 1898; Faussek, 1899, 1901). According to Ziegler, the primitive coelomic cavities were open pouches for the accumulation of waste products; they were not diverticula of the archenteron, but were, perhaps, of the nature of protonephridia. The nephrocoele theory as modified by Faussek holds that the excretory coelomic sacs are not primitive structures in a phylogenetic sense, but that they have been developed for excretory purposes in the embryo, and are hence purely ontogenetic organs. Faussek supports his theory with the generalization that the open metanephridia constitute exits from the coelom, while the closed

protonephridia serve for removal of waste products from the haemocoel. This statement, however, is not entirely true, for in some of the Polychaeta protonephridia are associated with coelomic sacs, and the primary larval somites of the annelids do not have metanephridia. On the other hand, there can be no question that the coelomic fluid does contain waste products of metabolism.

A fourth theory, that of Kleinenberg (1886), identifies the primitive mesoderm with muscle tissue, and is thus more satisfactory than the other theories because it deals with the beginning of the mesoderm as a functional tissue. Kleinenberg attributes the idea of a muscle origin for the mesoderm to Rabl, who later discarded it, but the theory rests principally on Kleinenberg's studies of the development of *Lopadorhynchus*. Kleinenberg claimed that in the larva of *Lopadorhynchus* the mesoderm is derived directly from the ectoderm at the posterior end of the body, and that the ectodermal myoblasts, and the neuroblasts of the ventral nerve cords, arise from a common neuromuscular rudiment. The mesoderm bands, or "muscle plates," become divided into segmental myotomes consequent on metamerism of the body, and the myotomes give rise to the body musculature, including, according to Kleinenberg, the dorsal and ventral longitudinal muscles, the parapodial muscles, and the circular muscles of the body wall. Then follows a separation of the muscle plates into parietal and visceral layers in each somite, producing thus the paired coelomic cavities, the peritoneal linings of which are formed by the inner cells of the myotomes. Kleinenberg's theory of the origin of the mesoderm thus gives to metamerism a mechanical significance, since it explains body segmentation as an adaptation to more efficient locomotion. Certainly, when once established, the chief function of metamerism is effective movement of the body, and to this feature the segmented annelids owe their superiority over the unsegmented flatworms. A serious weakness of the muscle theory of the origin of the coelomic mesoblast, however, is found in the fact that so many tissues other than muscle are evolved from it. Muscle fiber is a highly specialized tissue, and it seems hardly likely that epithelial tissue, for example, would be formed from muscle cells, since ordinarily it is epithelial tissue that gives rise to muscle fibers and to the various other specialized tissues of the body. Furthermore, as shown by Meyer (1901), muscle is not formed from the coelomic mesoblast of *Lopadorhynchus* until after the segmentation of the mesoderm bands and the formation of the coelomic cavities.

The literature of annelid morphology is replete with discussions on the nature and difference of the "two kinds of mesoblast"; but

the facts concerning the ontogenetic origin of the annelid mesoblast apparently can be expressed in the simple statement that *mesoblastic tissue may be formed by internal proliferation from any part of the blastoderm*, and may, therefore, be both "ectodermal" and "endodermal." The mesoblast of the first three quartets of the blastula (see Torrey, 1903) gives rise to the so-called larval mesoblast, or mesenchyme; from the fourth quartet ordinarily arises the coelomic mesoblast, or mesoderm. That these two groups of mesoblast cells primarily have the same morphological status is indicated by the fact that in the Platyhelminthes they do not become differentiated into separate tissues. Surface (1907), who first followed the divisions of the $4d$ cell in a flatworm, shows that in *Planocera* the $4d$ blastomere gives rise to both endoderm and mesoblast as it does in the annelids, since, of the two cells of the first division, $4d^1$ (fig. 5 H) forms the endoderm (I, *End*), and $4d^2$ gives rise to two lateral groups of scattered mesoblast cells (I, *Msb*⁴), which are at first quite distinct from the mesoblast of the second quartet (*Msb*²), though eventually they intermingle with the latter to form the parenchymatous tissue of the adult. In *Planocera* the usual endodermal "macromeres" degenerate and almost the entire endoderm proceeds from the $4d^1$ cell. Finally, we may correlate the "double origin" of the annelid mesoblast with the production of muscle tissue from both the ectoderm and the endoderm in the Coelenterata.

From the condition in the Platyhelminthes, it becomes evident that the primitive mesoblast was a parenchymatous mass of undifferentiated cells occupying the haemocoel, which had been proliferated internally from both the ectoderm and the endoderm. In the unsegmented ancestors of the annelids, the ectodermal mesoblast must have formed a primary somatic muscular system, represented by the larval musculature of modern annelids, which is derived from the ectodermal quartets of the blastula. The principal part of the parenchyma, therefore, came to be that part of the mesoblast proliferated in the posterior part of the body, chiefly, or usually, from the $4d$ cell of the fourth quartet. The persistent parenchyma thus became the embryonic middle layer known specifically as the mesoderm.

Since the most important result of metamerism is the production of a mechanism of movement based on the division of the body into consecutive motor units, it can scarcely be questioned that metamerism had its origin as an adaptation to more effective body movement. Inasmuch as the evidence from embryonic development shows that metamerism originates ontogenetically in the ectoderm and its derivatives, and is secondarily imposed upon the mesoderm, we may

suppose that it took its inception phylogenetically from an attachment of the primary (ectodermal) longitudinal somatic muscles at consecutive rings on the body wall, and from the accompanying ingrowth of fibers that formed contractile dissepiments between the myotomes. The ingrowth of the septal muscles cut the parenchymatous mesodermal bands into segmental blocks. This modification and elaboration of the primitive muscular system, and the consequent segmental division of the mesoderm bands, give at once the essential quality of metamerism, and from it there follows as a necessary result the metamerization of other organs, such as external ectodermal structures, the ventral nerve cords, and all structures of mesodermal origin.

The coelomic cavities first appear in the annelid embryo or larva as cleavage spaces in the segmental mesoderm blocks. Since the unsegmented Platyhelminthes have nephridial organs, it may be assumed that the primitive annelids possessed simple segmental nephridia in the form of internally closed tubules extending into the haemocoel. The primitive coelomic cavities, therefore, were probably spaces formed in the segmented parenchyma for the accumulation of body fluid charged with excretory products. The inner cells of the parenchyma now formed epithelial walls about the nephric cavities, which became the coelomic sacs; the outer cells were converted largely into muscles and connective tissue. The muscle cells gave rise to fibers that reinforced the somatic musculature, and eventually came to be its principal constituents. The definitive musculature of modern annelids, therefore, is a composite of fibers derived from the larval ectoderm and of fibers formed from the coelomic mesoblast, but in the Onychophora and the Arthropoda the entire musculature appears to be now a coelomic product. There is no reason necessarily for supposing that the primitive mesodermal muscles were functional elements of the coelomic sacs, for, though in ontogeny the mesoderm usually takes the form of two-layered bands of cells, within which the coelomic cavities are formed, it would seem probable that the primitive mesoderm was a loose parenchymatous tissue. The coelomic sacs are specifically the epithelial walls formed about the nephric cavities; the surrounding muscles were probably generated from the outer undifferentiated cells of the original parenchyma.

With the later development of the teloblastic somites, into which the germ cells were distributed from their posterior source of proliferation, the reproductive products were discharged into the coelomic sacs of these somites, which thus became gonocoelic as well as nephrocoelic in function. Open nephridia or coelomoducts now connected the coelomic cavities with the exterior and served both as excretory

and as genital outlets. Finally, in the Onychophora and the Arthropoda, the coelomic sacs have been divided into gonadial compartments and nephridial compartments, which have become reduced in size and limited to restricted parts of the body, with the result that the haemocoel is restored as the functional body cavity.

III. DEVELOPMENT OF THE ANNELID NERVOUS SYSTEM

The annelids and the arthropods undoubtedly have a closer bond of union in the structure of the nervous system than in any other feature of their organization, except metamerism itself. The definitive central nervous system of the polychaete annelids is developed from two distinct sources, one located in the prostomium, or episphere of the trochophoral larva, the other in the somatic region, or hyposphere of the larva. From the first is produced the brain; from the second, the ventral nerve cords. The nervous system of the trochophore consists of ganglionic centers in the prostomium connected by circular and radial nerve tracts, from which trunks proceed into the hyposphere (fig. 4 A). This primary system centering in the prostomium must represent the primitive neural system of the unsegmented ancestors of the annelids, adapted to the structure of the trochophoral larva, and is probably congenetic in its origin with the nervous system of the Platyhelminthes. The segmentally ganglionated ventral nerve cords of the postoral region of the trunk are correlated in their development with the development of body metamerism; they pertain, therefore, to a later stage of evolution, and have no homologues in the unsegmented worms. The definitive connection between the prostomial and somatic parts of the nervous system is established secondarily in the ontogeny of the polychaetes, but in the oligochaetes the two parts are said to be continuous from their inception. The fundamental structure of the somatic nervous system of the articulate animals is an adaptation to the function of regulating the muscular mechanism of metameric body movement; the prostomial system is primarily sensory in function, except insofar as it controls the movements of prostomial appendages.

The phylogenetic origin of the articulate nervous system can probably be interpreted very closely from the development of the neural elements in the trochophore larva of the polychaete annelids, and must have been about as follows: The primary neurocytes were probably sensory cells of the ectoderm closely associated with the primary myocytes, and were thus, at first, both receptive and motor in function. As the muscular system became elaborated, however, the primary neurocytes were withdrawn to the inner surface of the ectoderm,

while other superficial cells assumed the receptive function and transmitted secondarily the impulses from external stimuli to the first set of cells, which now became purely motor neurones. Finally, still other neurocytes gave rise to a subepidermal plexus of fibrous tracts that formed lines of intercommunication between the scattered motor and sensory elements, and thus unified and coordinated the entire nervous system. Then the nerve cells of the prostomial region became aggregated into a number of ganglionic centers, principally associated with groups of receptive cells in primitive sensory organs, and the nerve

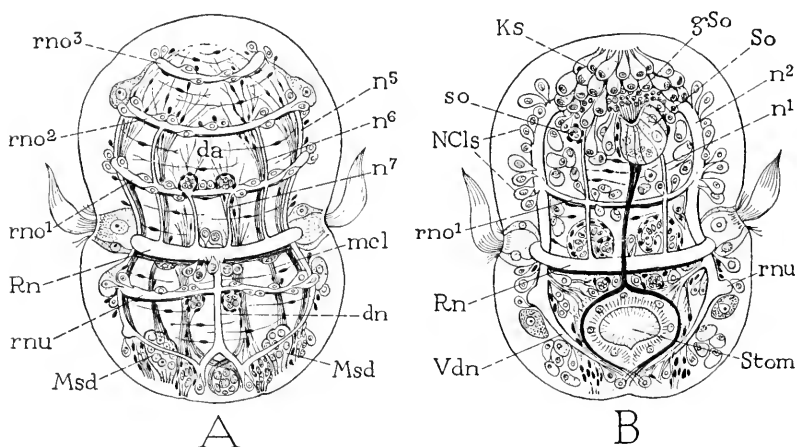


FIG. 8.—The nervous and muscular elements of a young trochophore larva of *Lopadorhynchus*, nerve tissue represented in white, muscle tissue in black. (From E. Meyer, 1901.)

A, aboral surface of larva. B, oral surface.

da, rudiments of so-called dorsal antennae; *dn*, median dorsal nerve of hyposphere; *gSo*, ganglion of left ciliary organ; *Ks*, apical plate; *mcl*, muscle fibers; *Msd*, mesoderm; *n*, longitudinal nerves (seven pairs in episphere); *NCl's*, nerve cells; *Rn*, circular nerve of prototroch; *rno¹*, *rno²*, *rno³*, circular nerves of episphere; *rnu*, circular nerve of hyposphere; *So*, left ciliary organ; *so*, rudimentary right ciliary organ; *Stom*, stomodaeum; *Vdn*, larval stomodaeal nerve.

tracts assumed definite courses. Thus was evolved the primary nervous system of the polychaete larva. The prostomial ganglia of this system later coalesce to form the definitive brain. The somatic nervous system, subsequently developed in correlation with metamerism, took its origin from restricted ventrolateral tracts of the somatic ectoderm, became connected with the brain, and finally replaced the primary system in the body region.

The most primitive nerve center of the annelids probably is represented by the apical ganglion of the polychaete trochophore (fig. 4 A, *ApGng*) situated beneath the ectodermal apical plate (*ApPl*), which

usually bears a tuft of cilia, and with which there may be associated a pair of small larval tentacles, and sometimes a pair of "eye spots." From the apical ganglion, nerves radiate posteriorly (LNv) on the inner surface of the epidermis, and these longitudinal radial nerves are connected by bands of circular fibers (CNv), chief of which is the nerve ring of the prototroch ($Prtr$). The nerve tracts, both radial and circular, closely follow the peripheral muscle bands of the larva (fig. 8), thus attesting that the nervous and contractile elements arose from common ectodermal neuromuscular rudiments. The nerve tissue is situated between the muscle fibers and the epidermis, the nerve cells being scattered individually, or condensed in small ganglionic groups.

The nervous system of the polychaete trochophore is best known from the elaborate studies of Kleinenberg (1886) and of E. Meyer (1901) on the larval development of *Lopadorhynchus*, a small errant polychaete of the family Phyllodocidae (fig. 13 D) having two pairs of prostomial tentacles but no palpi. The larva of *Lopadorhynchus* is a typical trochophore (fig. 8) with an equatorial band of cilia, the prototroch, just above the mouth. The apical ciliary organ, however, does not have the usual form and position; it is transposed to the anterior ventral surface, and is divided into a well-developed organ on the left (B, So), and a rudimentary organ on the right (so). The episphere contains seven pairs of longitudinal nerves (n^1-n^7), and is encircled by three nerve rings (rno^1-rno^3) above that of the prototroch (Rn). In the hyposphere there is but a single nerve ring (A, rnu). The largest of the longitudinal nerves are two thick lateroventral nerve tracts (B, n^2), which anteriorly (apically) are continuous with each other in a wide transverse commissural arch within the episphere, and posteriorly are extended into the hyposphere as a pair of large lateral trunks (Vdn) that break up into smaller branching nerves.

The neural cells of the *Lopadorhynchus* larva are described in great detail by Meyer. In general they lie along the fiber tracts (fig. 8 B, $NCLs$), where many of them are aggregated into small ganglionic clumps, particularly in the episphere. In the early stages of development, according to both Meyer and Kleinenberg, the neurocytes are generated from the ectoderm in association with muscle cells, and the principal neuromuscular rudiments of the episphere represent larval sensory organs (fig. 16 A), of which the nerve cells (n) form small ganglionic centers. The scattered neurocytes are probably the generative cells of the fibers in the nerve tracts. The ganglionic centers of the larva pertain to the apical ciliary organs, a pair of transient larval antennae, the two pairs of persistent tentacles, which are dorsal and ventral in the adult (fig. 13 D), and the nuchal organs, but include

also two cell groups of unknown significance situated on the dorsal surface of the episphere (fig. 8 A, *da*). From some of the ganglion cells nerve processes go to the muscles, and from others fibers penetrate centrally into the nerve tracts.

Before the beginning of larval metamorphosis, Meyer says, the production of myocytes ceases in the larval neuromuscular centers, and during metamorphosis a large part of the larval musculature is

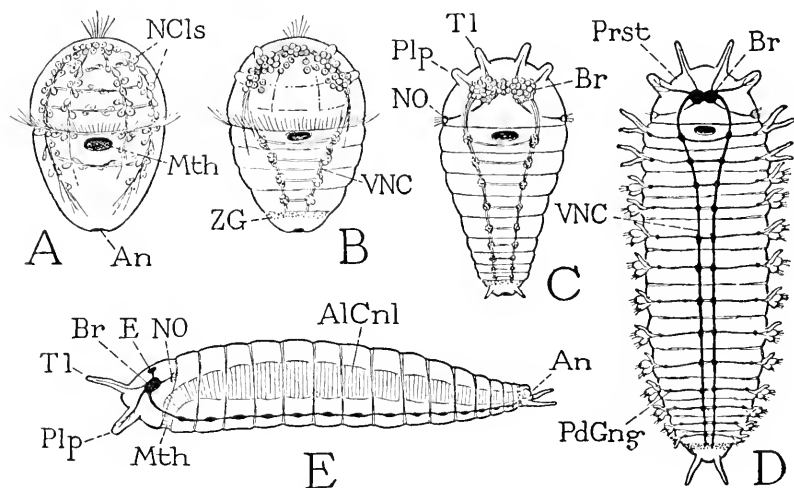


FIG. 9.—Theoretical evolution of the annelid nervous system, diagrammatically following Kleinenberg's and Meyer's accounts of the development of the nervous system in the larva of *Lopadorhynchus*.

A, early trochophore with diffuse nerve cells (*NCLs*) along the radial and circular nerve tracts. B, nerve cells of episphere concentrated in incipient ganglia connected with ectodermal sensory organs along lateral radial nerves; ventral nerve cords (*VNC*) developed from ectoderm of hyposphere. C, scattered ganglia of episphere condensed into a cerebral mass (*Br*); cerebral connectives united with ventral nerve cords. D, generalized adult nervous system; podial ganglia developed at bases of body appendages. E, nervous system of adult polychaete, lateral view.

AlCnl, alimentary canal; *An*, anus; *Br*, brain; *E*, eye; *Mth*, mouth; *NCLs*, nerve cells; *NO*, nuchal organ; *PdGng*, podial ganglion; *Plp*, palpus; *Prst*, prostomium; *Tl*, tentacle; *VNC*, ventral nerve cord; *ZG*, zone of growth.

lost. Many of the primary muscles, however, remain, including those of the persistent tentacles and nuchal organs, and certain other muscles of the prostomium. The neural cells of the various ganglionic centers of the larval episphere, on the other hand, increase in number until they become so crowded that details of their further development cannot be followed. The cells thus generated, however, are massed upon the large lateral nerve trunks of the episphere (fig. 8 B, *n*²) and their anterior commissure. In this manner there is formed from

numerous agglomerated centers in the larval episphere (fig. 9 A, B) a compact cellular and fibrous body of nerve tissue (C, *Br*), which becomes the brain of the adult worm (D). Hence, as Kleinenberg remarks, the developmental history of the brain in *Lopadorhynchus* shows how extraordinarily complicated in its origin is the cephalic ganglion even in the annelids. However, that details in the probable phylogenetic history of the nervous system are not necessarily recapitulated in ontogeny is shown in many annelids having a direct development, or one in which the trochophoral stage is passed within the egg, for in such forms the brain is differentiated from the

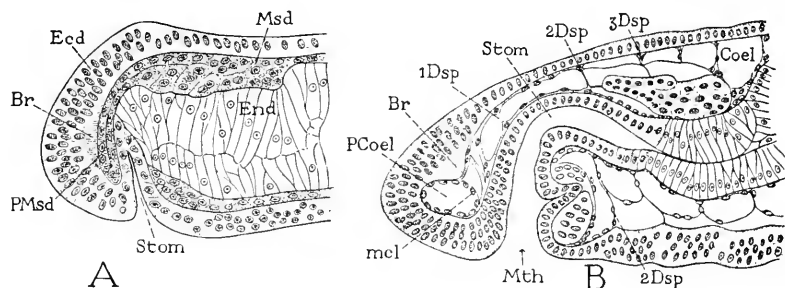


FIG. 10.—Median vertical sections of the anterior end of an embryo of the viviparous polychaete *Ctenodrilus branchiatus* Sokolow (Cirratulidae), showing extension of the mesoderm into the prostomium, and the direct development of the brain from the prostomial ectoderm. (From Sokolow, 1911.)

A, embryo before appearance of coelom, with mesoderm (*Msd*) extended into prostomium (*PMsd*). B, full-grown embryo, with coelom and dissepiments, coelomic cavity of prostomium (*PCoel*) continuous with coelomic cavity of first postoral somite (metastomium), which in the embryo is separated from second somite by a temporary dissepiment (*1Dsp*).

Br, brain; *Coel*, coelom; *1Dsp*, first (temporary) dissepiment, behind first postoral somite; *2Dsp*, *3Dsp*, second and third (permanent) dissepiments; *Ecd*, ectoderm; *mcl*, muscles; *Msd*, mesoderm; *Mth*, mouth; *PCoel*, prostomial coelom; *PMsd*, prostomial mesoderm; *Stom*, stomodaeum.

prostomial ectoderm as a single, compact mass of neural cells (fig. 10, *Br*).

The larval innervation of the hyposphere gives way during metamorphosis to the definitive body nervous system, consisting of the ganglionated ventral nerve cords and their peripheral nerves. The rudiments of this system appear first in the embryo as continuous strands of neurocytes proliferated in the ventral parts of the ectodermal somatic plate as the median edges of the latter unite to close the blastopore. The cords later become ganglionated by the segmental aggregation of their cells. The neuroblasts of the somatic nerve cords, Meyer believes, represent the nerve cells of a series of primitive ectodermal sense organs. Though there are no persistent remnants of

such sensory organs in the annelids, the so-called "ventral organs" of the Onychophora, from which the nerve cords are differentiated, suggest that the latter took their origin from ectodermal structures of some kind.

The final connection between the brain and the ventral nerve cords, according to Kleinenberg and Meyer, is established by fibers that grow forward from the first ventral ganglia (fig. 9 B) and unite with the lateral nerve trunks (fig. 8 B, *Vdn*) extending posteriorly from the arms (n^2) of the cerebral commissure. The union thus formed produces the stomodaeal (circumoesophageal) connectives, through which the prostomial and somatic nerve centers are unified in the definitive nervous system.

The peripheral subcutaneous nervous system of the adult worm is developed directly from scattered neurocytes of the ectoderm. To this system Kleinenberg ascribes the parapodial ganglia (fig. 9 D, *PdGng*), which, he says, are formed quite independently of the central system by groups of ectodermal neurocytes situated mesad of the parapodial bases. Secondly, the parapodial ganglia send connecting nerves to the ventral nerve cords.

IV. THE ADULT ANNELID

The final development of the adult polychaete annelid from the larva depends upon the histogenic activity in the zone of undifferentiated cells situated between the last larval somite and the pygidium (fig. 11 B, *ZG*). Within this *zone of growth* is generated anteriorly a series of secondary postlarval somites (C, D), which does not represent an extension of the body, but an expansion of a small part of it, since the new somites are interpolated between the primarily segmented larval body and the pygidium. The more anterior somites of the new series, being those first formed, are the first to acquire the mature structure. The teloblastic growth-process is the same whether the larva is a typical trochophore (fig. 12 B, D), or one more nearly resembling the adult worm (E, F, G), but in the first case a greater degree of metamorphosis accompanies the formation of the new somites. Hence, though we may eliminate the trochophore from our concept of the primitive annelid, we cannot dismiss the secondary formation of the teloblastic somites as a purely ontogenetic process—it must be explained in terms of phylogeny.

THE TELOBLASTIC, OR POSTLARVAL, SOMITES

The zone of growth, as described by Lillie (1906) in *Arenicola cristata*, is a mass of large clear mesodermal and ectodermal cells,

which are frequently to be seen in the process of mitosis. Posteriorly the growing zone is sharply defined from the pygidial region, but anteriorly it passes by gradual transition into the more fully differentiated region in front. Its ectodermal cells, Lillie says, must be derived from the last transverse row of cells in the ectodermal somatic plate produced from the *2d* cell of the embryo. The space between the ectoderm and the endoderm is filled with a mass of mesoderm cells very probably generated from the mesodermal teloblasts. Anteriorly the mesoderm of the growing zone is shut off by a roughly defined

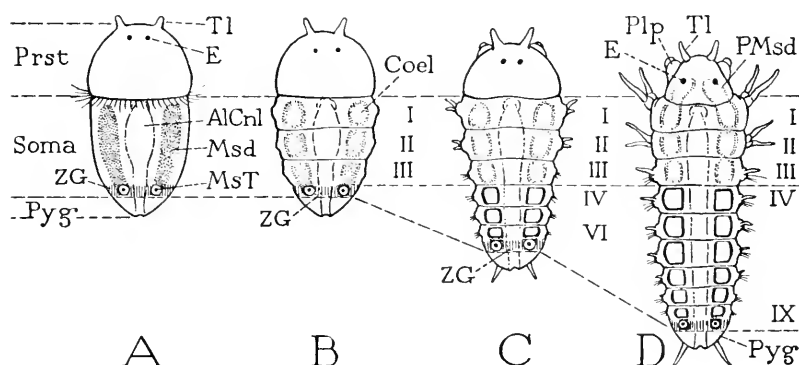


FIG. 11.—Diagrams illustrating the direct primary segmentation of the body of a larval polychaete, and the growth of the worm by successive addition of secondary teloblastic somites generated in the subterminal zone of growth.

A, larva with unsegmented soma and mesoderm bands. B, larval soma and mesoderm directly segmented. C, D, successive formation, from subterminal zone of growth, of teloblastic somites interpolated between primary larval somites and terminal pygidium.

AlCnl, alimentary canal; *Coel*, coelomic cavity; *E*, eye; *I-III*, primary larval somites; *IV-IX*, secondary teloblastic somites; *Msd*, mesoderm; *MsT*, mesodermal teloblast; *Plp*, palpus; *PMsd*, prostomial mesoderm; *Prst*, prostomium; *Pyg*, pygidium; *Soma*, body region between prostomium and pygidium in which somites are formed; *Tl*, tentacle; *ZG*, zone of growth at end of soma.

transverse partition from the coelomic cavity of the somite before it. The first evidence of new somite formation is the appearance of an irregular space in the mesodermal mass of the zone of growth, which enlarges upward around the alimentary canal and becomes the coelomic cavity of the new somite. (*Arenicola* has a dorsal mesentery but none beneath the alimentary canal.) The anterior coelomic wall is pressed against the preceding partition and becomes the posterior lamella of the dissepiment thus formed. Longitudinal muscle fibers make their appearance at an early period in the somatic layers of the mesoderm, but the circular muscles, Lillie claims, appear much later, and evidently, as described by Meyer (1901), are derived from

the inner surface of the ectoderm. According to Iwanoff (1928) the mesoderm of the postlarval somites is formed in *Polygordius*, *Aricia*, *Arenicola*, and the Oligochaeta from the mesodermal teloblasts that generate the larval bands of mesoderm, but in the rest of the Polychaeta the postlarval mesoderm is proliferated from the ectoderm of the zone of growth.

The pygidial region posterior to the zone of growth retains its primitive characters throughout the course of development, and is carried continuously backward as the number of somites increases. When the definitive number of somites has been formed, the growing zone loses its distinctive features and becomes indistinguishable as such. Structurally the secondary, or teloblastic, somites are modeled according to the general plan of the primary somites before them; but, though they may differ in various structural details from the latter, they have one distinctive feature, which is that they alone contain the germ cells. Germinal centers ("gonads") may occur in all the teloblastic segments, but in most of the polychaetes they are limited to a definite part of the body (the epitoke), and in the oligochaetes they are usually restricted to a few segments.

The ancestral annelids necessarily were reproductive as adults in all their evolutionary stages, but phylogenetic forms recapitulated in ontogeny are generally not reproductive. Hence, it is difficult to study the evolution of the reproductive system from ontogenetic development. The germ cells of the annelids usually are not recognizable as such in the larva, and little is known of their embryonic origin. It is claimed by Malaquin (1925), however, that in the serpulid *Salmacina dysteri* the sex elements first appear as differentiated cells in the gastrula, and that later (Malaquin, 1924) these cells become localized immediately before the zone of growth in the posterior segments of the young larva, where they lie ventral to the rectum, and are distinguishable from the surrounding cells by their large, clear, spherical nuclei containing numerous small chromatic masses. In the oligochaete *Pachydrius*, Penners (1930) claims the germ cells arise directly from the mesodermal teloblasts, and are the first cells formed by the latter. The germ cells, as shown also by Penners and Stäblein (1930) in Tubificidae, appear prior to the formation of the definitive gonad somites, and migrate in the haemocoel to these somites, where they penetrate the mesoderm and finally take their definitive positions in the dissepiments. It seems highly probable, therefore, that the primitive annelids, at a phylogenetic stage before the teloblastic somites were formed, carried the germ cells in the undifferentiated posterior part of the body behind the last primary

somite. From this point the germ cells must have been distributed to the secondary somites when the latter began to be developed during the course of evolution. Hence, primarily, the entire series of teloblastic somites would appear to have been genital segments.

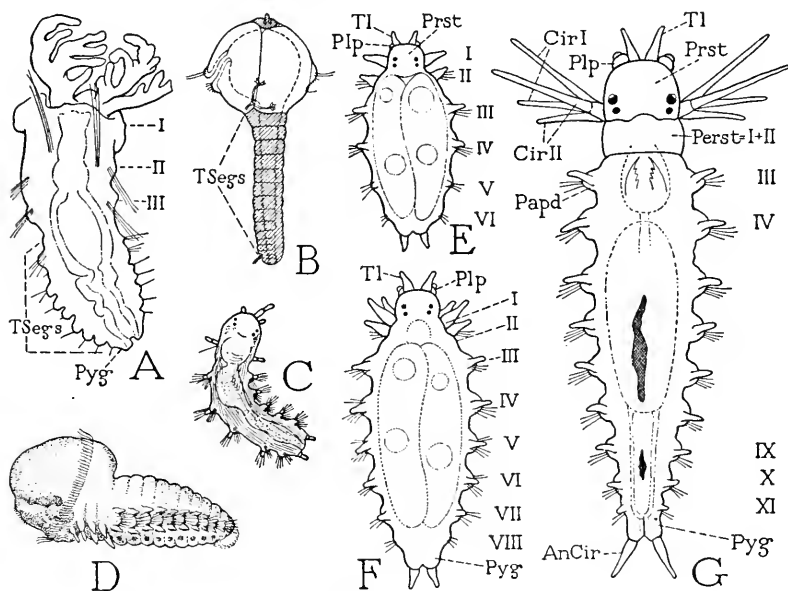


FIG. 12.—Examples of the growth of larval Archiannelida and Polychaeta by proliferation in a subterminal zone of growth of teloblastic segments added to the primary larval body.

A, larva of *Eupomatus uncinatus* with series of teloblastic, or "postlarval," segments (*TSegs*) interpolated between the three primary larval somites (*I*, *II*, *III*, see fig. 7 A, B) and the terminal pygidium (simplified from Iwanoff, 1928). B, larva of *Polygordius neapolitanus* Fraipont during metamorphosis, with series of teloblastic segments added to the trochophoral body, which is itself unsegmented and contains no primary mesoderm (from Woltereck, 1905). C, half-grown young of *Nerilla antennata* Schmidt (from Schlieper, 1925). D, larva of *Lopadorhynchus brevis* Grube with series of teloblastic segments (from Kleinenberg, 1886). E-G, growth stages of "hereidogen" larva of *Platynereis dumerilii* Aud. & Milne-Edw. (from Hempelmann, 1911, see also fig. 7 C, first stage larva).

AnCir, anal cirrus; *CirI*, *CirII*, tentacular cirri of first two somites, united in peristomium; *I-XI*, somites; *Papd*, parapodium; *Perst*, peristomium; *Plp*, palpus; *Prst*, prostomium; *Pyg*, pygidium; *Tl*, prostomial tentacle; *TSegs*, teloblastic segments.

A condition similar at least to that which we should expect to find in the primitive annelids is seen in the archiannelid *Dinophilus* (fig. 13 A). The body of *Dinophilus* consists of six or seven somites clearly defined externally between the prostomium and the pygidium, but there are no coelomic cavities in the diffuse mesoderm of the

somites anterior to the last one, though each of these somites has a pair of simple protonephridia. In the terminal somite are formed the reproductive organs, which, in the female, consist of a delicate gonadial sac, either single or double, extending forward in the body, and opening posteriorly by a median pore, at least at the time of egg laying. The gonadial sac appears to represent the coelom of the last segment, though, as Iwanoff (1928) points out, it may be simply a space accommodating the germ cells in the undifferentiated tissue near the end of the body. Hence, the apparent last somite is either a single teloblastic genital somite, or a region corresponding with the zone of growth of the polymerous annelids.

A concrete example of the secondary distribution of the germ cells in a polymerous annelid is given by Malaquin (1924 a) in his study of the development of *Salmacina dysteri*. The germ cells, as we have seen, are first localized in the growing zone of the young larva. When the formation of the postlarval segments begins, Malaquin says, the germ cells multiply, and three, four, or five of the resulting gonocytes become adherent to the outer wall of each new coelomic sac. Thus the germ cells, proliferated from a constant source, are distributed to the newly forming somites, and are extracoelomic both in their origin and in their secondary segmental positions. After a period of inactivity the segmentally distributed gonocytes begin to multiply in the coelomic walls, and here form the small masses of germinal cells ensheathed in peritoneal folds that are known as the "gonads."

If, now, the ontogenetic facts of annelid growth are given a phylogenetic significance, it becomes evident, as claimed by Iwanoff (1928), that the extension of the worm by the teloblastic generation of new somites, in which are apportioned groups of the multiplying germ cells, was primarily a means of amplifying the reproductive function. In the course of evolution it gave rise to a type of animal from which have been derived the modern Annelida, the Onychophora, and the Arthropoda.

The teloblastic genital segments are in many respects mechanical improvements over the primary segments; their muscular equipment is stronger, the parapodia better constructed for locomotion, the dissepiments usually more complete, and the nephridia more efficient for excretory purposes. Hence, the whole worm is clearly a stronger and a more active animal by reason of the addition of the well-organized reproductive somites. At the bottom of the water the creeping worm is better able to force its way under stones or into crevices, or to burrow into sand or mud; but at the breeding season

its new powers of locomotion come into effective service, for now many modern species that habitually live at the bottom rise to the surface in swarms of energetically swimming individuals, both males and females, and here discharge the matured gametes.

That the genital segments may be of no special physiological importance to the worm, except for carrying, maturing, and distrib-

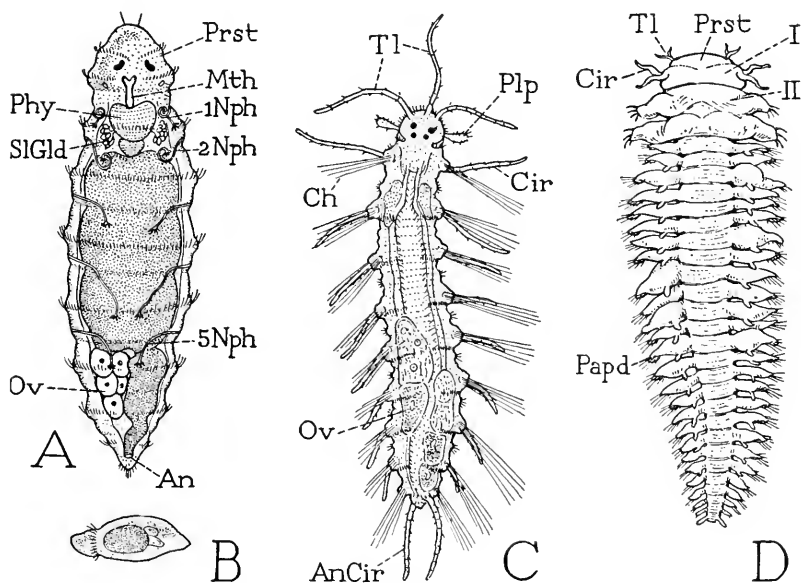


FIG. 13.—Examples of annelid types.

A, B, *Dinophilus*, a very simple archiannelid, perhaps a primitive form, lacking teloblastic somites, tentacles, cirri, chaetae, parapodia, and coelomic sacs; with five pairs of protonephridia, reproductive organs in posterior part of body (A, *D. gyrotilatus* Schmidt, adult female; B, adult male, from Shearer, 1912). C, *Nerilla*, an archiannelid with polychaete characters, perhaps a degenerate form, having a coelom, open metanephridia, and direct development (fig. 12 C) (*N. antennata* Schmidt, from Goodrich, 1912). D, *Lopadorhynchus*, an errant polychaete (Phyllodocidae), having typical trochophoral development (fig. 8) with metamorphosis (fig. 12 D) producing long series of teloblastic somites (*L. uncinatus* Fauvel).

An, anus; AnCir, anal cirrus; Ch, chaetae; Cir, cirrus; I, II, first two somites; Mth, mouth; Nph, nephridium; Ov, ovary; Papd, parapodium; Phy, pharynx; Plp, palpus; Prst, prostomium; SIGld, salivary gland; Tl, tentacles.

uting the reproductive elements, is shown by the various ways in which the annelids can dispose of these segments without otherwise impairing their functional integrity. There is the well-known case of the palolo worms, *Eunice fucata* and *E. viridis*, for example, which live in crevices of rocks at the bottom of the water, and at the time for spawning detach the rear parts of their bodies, already

loaded with the mature generative elements. The reproductive tail-ends (epitokes) then actively swim to the surface, where myriads of them congregate to liberate the gametes. In their accustomed haunts the anterior nonreproductive sections (atokes) regenerate the discarded epitokes in preparation for next year's consignment to the breeding grounds. Various other species of Polychaeta have similar habits. The Syllidae are famous for the many forms of schizogenesis, strobilation, and budding that take place among them, but here the detached piece, either before or after separation, generates a new head and becomes a complete worm except perhaps for the lack of an alimentary canal and a few other unimportant structures. Again, in some of the Ctenodrilidae the worm breaks up by constriction into several pieces of a few segments each, and the middle pieces regenerate both a head and a tail.

The periodic fragmentation of the body for reproductive purposes, however, cannot lead to anything in the way of constructive evolution, and, with the annelids in general, the tendency has been to integrate the entire series of somites into a mechanical and physiological unit, in which the reproductive cells are assigned to definite segments. In the Arthropoda, though the body may still be composed of freely movable segments, the process of integration has been carried so far, and the various organs so interdependently distributed, that fission becomes impossible without fatal results. It would seem, therefore, that the teloblastic somites, first added apparently for reproductive efficiency, have been found so useful in other ways that they have come to constitute not only the largest part of the body in all the articulate animals, but its most important part, except for the primary sensory and nervous elements contained in the head.

A structural differentiation between groups of somites, forming distinct body regions, or tagmata, has taken place in many of the polychaetes, particularly in the Sedentaria, and is a characteristic feature of all the Arthropoda. The zone of growth, therefore, which presumably at first gave rise to a series of identical somites, has acquired the remarkable faculty of differential activity, producing successively, at definite segment intervals, two or more series of somites having often a strongly contrasting structure, while minor differences may be distributed throughout the entire series of segments.

THE PROSTOMIUM AND ITS APPENDAGES

The annelid prostomium is the part of the trunk that is not invaded by the blastopore as the latter elongates forward on the ventral sur-

face of the embryo (fig. 6 D, *Prst*); in the adult it is reduced to a small lobe overhanging the mouth (fig. 14, *Prst*). Appendages of the prostomium are best developed in the errant polychaetes, where typically they include a pair of anterior tentacles, or "antennae" (*Tl*), with frequently a median tentacle between them, and a pair of more posterior and ventral palpi (*Plp*). The prostomial appendages are clearly not equivalent to the parapodia of the postoral body somites, but they have the same development in the larva as the parapodial cirri (cf. fig. 16, A and B). Since the prostomium usually contains the brain and bears the apical sense organs, it constitutes the "head" of the worm. In the absence of prostomial appendages and sense

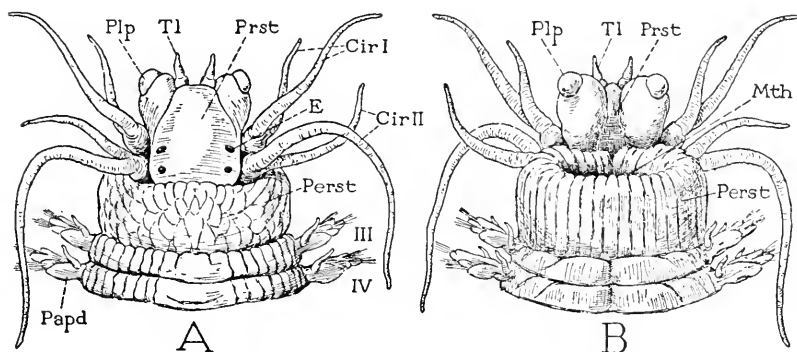


FIG. 14.—Head and anterior body segments of *Nereis virens* Sars. A, dorsal; B, ventral.

Cir I, *Cir II*, tentacular cirri of first and second somites united in peristomium; *E*, eye; *III*, *IV*, third and fourth somites; *Papd*, parapodium; *Perst*, peristomium (somites I and II); *Plp*, palpus; *Prst*, prostomium; *Tl*, prostomial tentacle.

organs, however, the brain may be secondarily withdrawn into the body, as in the earthworms (fig. 17 C, D, *Br*).

The prostomium is not affected by the process of metamerism that cuts the postoral body region into a series of somites. Since the mesoderm bands of the larva do not proceed anterior to the mouth (fig. 6 F), the larval prostomium does not contain mesoderm; but in later stages the mesoderm of the first somite may be extended into the prostomium (fig. 10 A) and give rise to a cephalic coelom and peritoneum (B, *PCoel*). Ordinarily the cephalic mesoderm is not segmented, but according to Binard and Jeener (1928) there is present in the prostomium of the spionid *Scolecopsis fuliginosa* a pair of distinct coelomic sacs, which are continuous with the cavities of the palpi, and have no connection with the coelomic sacs of the first postoral somite. This fact, the authors point out, gives a new argu-

ment in favor of the homology of the polychaete palpi with the tentaclelike antennae of the Onychophora; but evidently it does not prove their further contention (1929) that the palpi are appendages of a secondarily "cephalized" somite, since it must first be demonstrated that coelomic cavities may not pertain to the preoral mesoderm itself.

THE BODY AND ITS APPENDAGES

The body of the annelid is the segmented part of the trunk posterior to the acronal prostomium, including the region of the true somites, the zone of growth, and the pygidium; but the term *soma*, in a restricted sense, would apply literally only to the region of the *somites* between the prostomium and the zone of growth or the pygidium. In the Polychaeta the first two somites are generally united with each other in a double segment known as the *peristomium* (fig. 14, *Perst*), the tentaclelike cirri of which (*CirI*, *CirII*) take an anterior position closely associated with the prostomium. The "cephalization" of the anterior segments in the polychaetes, therefore, contrasts with that in the arthropods, since, with the latter, the first stage of cephalization is a union of the first somite with the prostomium. In the oligochaetes, however, the first somite and the prostomium may unite to form a composite head as in the arthropods.

The fundamental demarcation of the annelid somites is the attachment of the longitudinal muscle fibers of the body wall and the muscles of the dissepiments on transverse circular grooves of the integument; but the coelomic sacs when present are strictly intra-segmental, and most of the ectodermal and mesodermal organs are segmentally repeated. The locomotor mechanism of the annelids consists primarily of the somatic musculature and the regulating nerve ganglia, which give movement to the body wall, but it usually includes external adjuncts in the form of bristles or chaetae, and, in the Polychaeta, lobelike segmental appendages, the parapodia. The annelid body musculature should be the basis of the derived arthropod musculature, but there is reason to doubt that the polychaete parapodia are prototypes of the arthropod legs.

The somatic musculature of the annelids includes the muscles of the body wall, the muscles of the chaetal sacs, and the muscles of the parapodia. The muscle fibers, with possibly rare exceptions, are of the nonstriated type. The musculature of the body wall is of a very simple pattern, so far as the arrangement of the fibers is concerned, but it may attain a strong development in the rapacious polychaetes and the burrowing oligochaetes. The longitudinal muscles

can produce only contraction or lateral undulatory movements of the body; the circular muscles are constrictors producing peristaltic waves of body compression, and longitudinal extension of the body by the creation of internal pressure. The arthropod type of body mechanism, involving intersegmental movement of integumental plates, can be derived from the intrasegmental annelid mechanism only by the establishment of new intersegmental divisions.

The polychaete somatic musculature is well developed in the Nereidae, of which *Nereis virens* may be taken as an example (fig. 15). The outermost layers of body wall muscles consist of fine circular fibers closely adherent to the integument (A, D, 1). Internal to these there may be bands of oblique fibers (D, 2) crossing each other in opposite directions. The largest of the somatic muscles, however, are four thick bundles of longitudinal fibers (A, 3, 4) lying internal to the others, two dorsal and two ventral, the fibers of which are attached on deeply inflected intersegmented folds of the integument (D, *isf*). The longitudinal muscles of the terrestrial oligochaetes are continuous in a thick layer around the entire circumference of each somite, except where they are interrupted by the intrusion of the four chaetal sacs. Besides the muscles of the body wall there is in *Nereis* a double series of paired, obliquely transverse ventral muscles, one pair anterior and the other posterior in each segment (D, 5, 6), which extend outward and upward from the median ventral fold of the body wall (A) to the lateral intersegmental folds between the parapodial bases. The intersegmental folds give attachment also to the transverse or radial muscles of the intercoelomic dissepiments. Most of the other muscles of the body pertain to the chaetal sacs and the parapodia, and will be described in connection with the parapodia.

A typical polychaete parapodium is a lateral outgrowth of the body wall (fig. 15 A, *Papd*), flattened antero-posteriorly, and usually divided into a dorsal lobe and a ventral lobe, which again may be subdivided into secondary lobules. Each major lobe bears distally a fan-shaped group of long chaetae (B, *Ch*), and on its base a slender cirrus (*dCir*, *vcir*). The chaetae arise from the inner walls of chaetal sacs (C, *chS*), from each of which a long rod, the acicula (*Acic*), extends inward to give attachment to protractor and retractor muscles.

The larval rudiments of the parapodia represent the cirri and the chaetal sacs, and are differentiated as cellular bodies within the ectoderm. The rudiments of the cirri, as described by Kleinenberg (1886) and by Meyer (1901) in the larva of *Lopadorhynchus* (fig. 16 B, *dcR*, *vcR*), consist each of an outer layer of myoblasts (*m*) and an inner core of sensory nerve cells (*n*). The cirri in their origin,

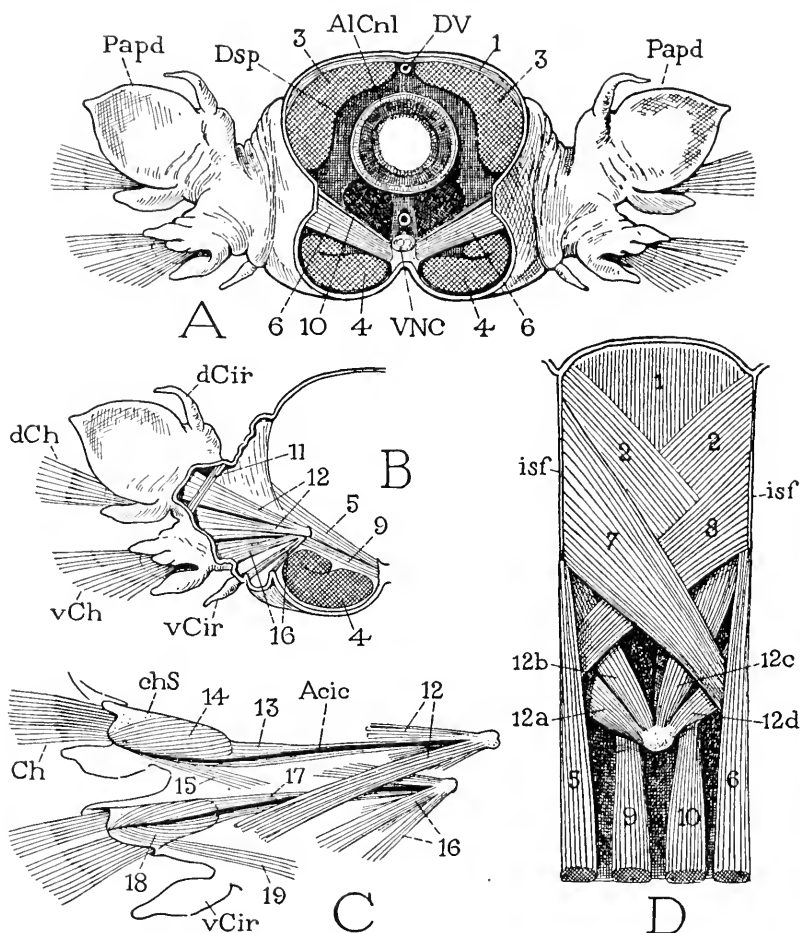


FIG. 15.—The polychaete locomotor mechanism: parapodia, and somatic and parapodial muscles of *Nereis virens* Sars.

A, transverse section of a body segment, posterior view, somewhat diagrammatic. B, a parapodium and its muscles, posterior view. C, chaetal apparatus of a parapodium. D, muscles of right half of a body segment, inner view.

Acic, acicula; *AlCnl*, alimentary canal; *Ch*, chaetae; *chS*, chaetal sac; *Cir*, cirrus; *dCh*, dorsal chaetae; *dCir*, dorsal cirrus; *Dsp*, intersegmental dissepiment; *DV*, dorsal blood vessel; *isf*, intersegmental fold of integument; *Papd*, parapodium; *vCh*, ventral chaetae; *vCir*, ventral cirrus; *VNC*, ventral nerve cord.

1, circular muscles of body wall; 2, oblique muscles of body wall; 3, dorsal longitudinal muscles; 4, ventral longitudinal muscles; 5, 6, anterior and posterior lateroventral, obliquely transverse muscles; 7, 8, dorsal motors of parapodium; 9, 10, ventral motors of parapodium; 11, intrinsic muscle of parapodium between dorsal and ventral lobes; 12, protractors of dorsal acicula and chaetal sac; 13, 14, retractor and protractor of dorsal chaetae; 15, retractor of dorsal chaetal sac and acicula; 16, protractors of ventral acicula and chaetal sac; 17, 18, retractor and protractor of ventral chaetae; 19, retractor of ventral chaetal sac.

therefore, resemble the tentacular rudiments of the prostomium (A), and later they grow out as tentaclelike processes. The bristle sacs are formed as ectodermal cell masses between the cirri (B, *chS*), the outer cells of which become myoblasts, while some of the inner cells enlarge and produce the chaetae; a lumen then appears in the cell mass, and the latter becomes an open eversible sac from which the chaetae protrude. Finally the cirri and the chaetal pouches are carried outward on an outgrowth of the body wall that becomes the principal part of the appendage. The mature parapodia of *Lopadorhynchus* are not of typical form in that each consists of a single lobe (fig. 16 C) with both chaetal sacs at its extremity.

In some of the polychaetes, particularly in the Sedentaria, there are two rows of podial organs on each side of the body (fig. 16 F), those of one series, the notopodia (*dPd*), being situated dorsolaterally, those of the other, the neuropodia (*vPd*), ventrolaterally. Each organ includes a cirrus (*Cir*) and a chaetal sac (*chS*), and is innervated separately from the corresponding podial ganglion (*PdGng*). In the Oligochaeta the podial organs are represented only by the chaetae, which usually are arranged in two separated rows on each side of the body. It is possible, therefore, that the usual two-branched parapodium of the Polychaeta (fig. 15 B) has been formed by the union of a notopodium and a neuropodium. Furthermore, the double composition of each notopodium and neuropodium suggests that the primitive polychaetes had dorsolateral and ventrolateral rows of cirri, and between them on each side two series of chaetal sacs. On the peristomial segments of adult polychaetes generally only the cirri are present (fig. 14 A, *CirI*, *CirII*), but on the rest of the body segments the chaetae-bearing lobes are usually the more important podial elements.

The musculature of a parapodium is somewhat complex: it includes extrinsic muscles that move the appendage as a whole, and intrinsic muscles concerned principally with the movement of the chaetae. In *Nereis virens* there are four extrinsic muscles for each parapodium, two dorsal (fig. 15 D, 7, 8), and two ventral (9, 10). The dorsal muscles arise anteriorly and posteriorly on the body wall, but cross each other obliquely to opposite margins of the parapodial base. The ventral muscles take their origins on the median infold of the ventral wall of the body segment (A), and extend laterally and dorsally, above the ventral longitudinal body muscles (4), to the anterior and posterior margins of the base of the parapodium. If the dorsal and ventral muscles inserted anteriorly act in opposition to those inserted posteriorly, the parapodium is moved anteriorly and posteriorly on

the vertical axis of its base, and this is the usual motion of the appendage; but the latter can also be lifted and depressed, and the up-and-down motion evidently results from an antagonistic action

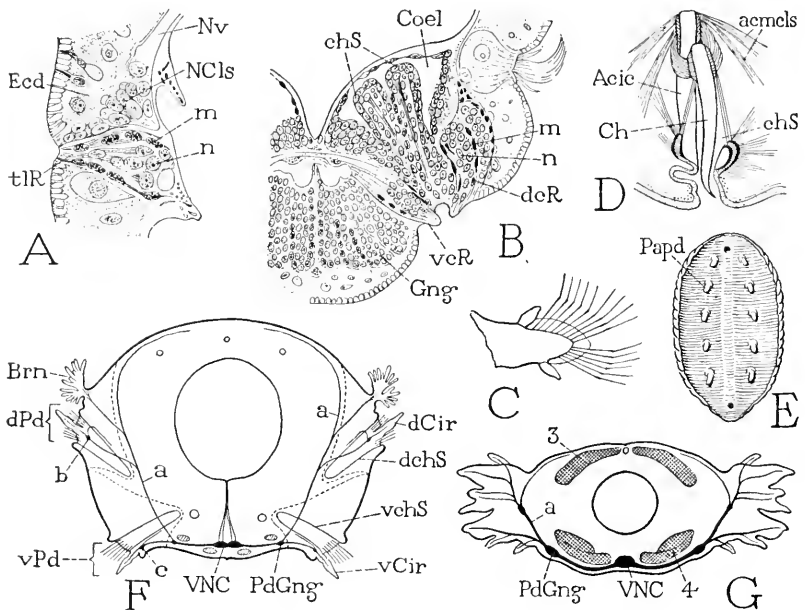


FIG. 16.—Development, structure, and innervation of the polychaete appendages.

A, section through larval rudiment of persistent dorsal tentacle (*tlR*) of trochophore of *Lopadorhynchus* (from E. Meyer, 1901). B, transverse section of larva of *Lopadorhynchus* through rudiments of a pair of chaetal sacs (*chS*) and associated cirri (from Meyer, 1901). C, parapodium of adult *Lopadorhynchus*. D, structure of the armature of a parapodium of *Myzostomum asteriac* Marinzeller, diagrammatic (from Stummer-Traunfels, 1903). E, a myzostomid, ventral view, showing parapodia. F, diagrammatic section of an amphionomid, *Hermodice carunculata* Pallas, showing widely separated notopodia (*dPd*) and neuropodia (*vPd*) and their innervation (from Storch, 1913). G, section of *Nereis virens* Sars, showing innervation of parapodia (from Hamaker, 1898).

a, lateral nerve from podial ganglion; *Acic*, acicula; *acmcls*, acicular muscles; *b*, notopodial ganglion; *Brn*, branchia; *c*, neuropodial ganglion; *Ch*, chaeta or chaetae; *chS*, chaetal sac; *Coel*, coelom; *dCir*, dorsal cirrus; *dcR*, dorsal cirrus rudiment; *dPd*, notopodium; *Ecd*, ectoderm; *Gng*, ventral ganglion; *m*, primary muscle cell; *n*, primary neural cell; *NCLs*, nerve cells; *Nv*, nerve; *Papd*, parapodium; *PdGng*, podial ganglion; *tlR*, rudiment of tentacle; *vcR*, ventral cirrus; *vcR*, ventral cirrus rudiment; *VNC*, ventral nerve cord; *vPd*, neuropodium; *3*, dorsal muscles; *4*, ventral muscles.

between the dorsal and ventral muscles. The intrinsic muscles of the parapodium include protractors and retractors of the chaetal sacs. The principal protractors (B, C, 12, 16) converge from the parapodial walls upon the inner ends of the acicular processes of the sacs (B,

C, D), but the sacs themselves are eversible by muscles in their own walls (C, 14, 18). A retractor (15, 19) arising within the parapodium is inserted on the distal part of each chaetal sac, and a muscle (13, 17) from the acicula, attached on the base of the sac, opposes the muscles (14, 18) that evert the sac itself.

The parapodia are subject to numerous structural modifications in the different groups of Polychaeta, and among the specialized types the small leglike parapodia of the Myzostomidae (fig. 16 E) are of particular interest because of their resemblance to the legs of Onychophora. Each myzostomid appendage, as described by Stummer-Traunfels (1903), contains a deep apical pouch (D, *chs*), from the inner end of which a large hooked process (*Ch*) projects outward, while from its distal wall a thick rod (*Acic*) extends inward and gives attachment to protractor muscles (*acmcls*) and muscles inserted on the base of the hook. It is evident that the hook is a single, greatly enlarged chaeta, and the internal arm an acicula. The myzostomid "leg," therefore, is only a modified parapodium adapted for clinging to the crinoid hosts on which the Myzostomidae live, and has only a superficial likeness to the appendages of Onychophora (fig. 31).

THE NERVOUS SYSTEM

The central nervous system of the Polychaeta, as shown in the larval development, is produced from separate prostomial and somatic rudiments, which secondarily become united (fig. 9); in the Oligochaeta the two parts are said to be continuous from their inception. The definitive brain, whether formed from discrete ganglionic centers, as in *Lopadorhynchus*, or from a single generative zone of the prostomial ectoderm (fig. 10 A, B, *Br*), is always a compact organ, though it is generally bilobed (fig. 17 A) or differentiated into several consecutive parts (fig. 18 C). The ventral nerve cords in the more primitive condition found in most of the archiannelids and in various polychaete and oligochaete families are entirely separate, except for their connection by commissures (fig. 19 A, B), and in such cases the nerve tissue usually preserves a close contact with the ectoderm from which it is derived (C). More commonly, however, the paired ganglia of the cords are united in single median ganglia (fig. 17 C, D), giving the cords themselves a median position; but even in such cases the ganglia of one or more pairs carried by the divergent anterior ends of the cords may remain widely separated. The first pair of united ganglia on the cords constitutes the so-called "suboesophageal ganglion," but it is evident that this ganglion does not belong always

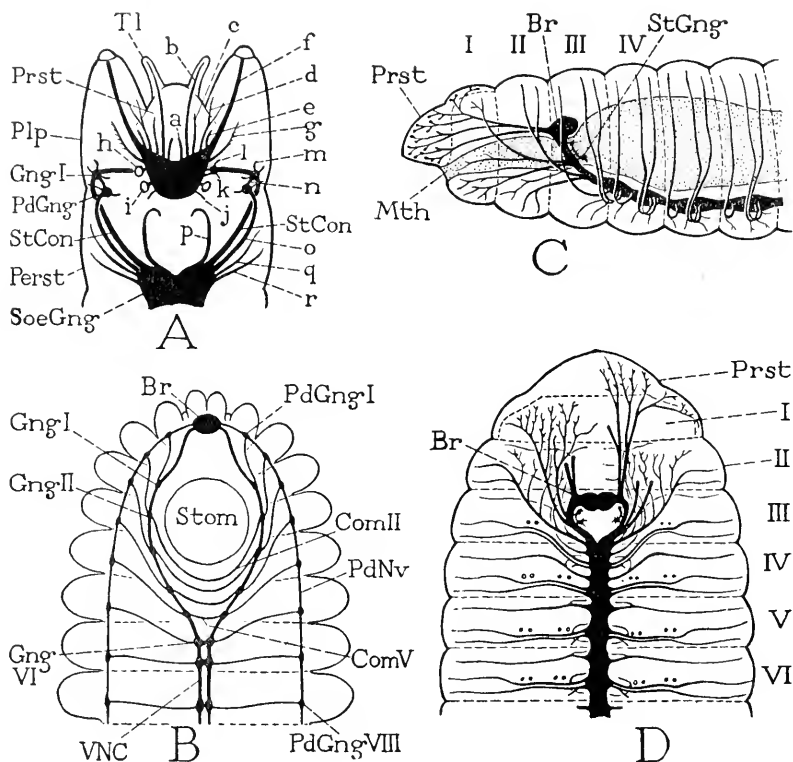


FIG. 17.—Nervous system of Annelida.

A, anterior nervous system of *Nereis virens* Sars, diagrammatic, showing nerves of cerebral and subesophageal ganglia (adapted from Hamaker, 1898). B, anterior nervous system of an amphinomid, *Hermodice carunculata* Pallas, showing podial nerves (*PdNv*) from brain connecting the podial ganglia, and divergence of ventral nerve cords (*VNC*) through several somites around stomodaeum (from Gustafson, 1930). C, anterior nervous system of *Lumbricus terrestris* Linn., lateral view, showing retraction of brain into third somite (simplified from Hess, 1925). D, same, dorsal view (from Hess, 1925).

Br, brain; *ComII*, *ComV*, commissures of second and fifth somites; *GngI*–*GngVI*, central ganglion of first to sixth somites; *I*–*VIII*, first to eighth somites; *Mth*, mouth; *PdGng*, podial ganglion of second peristomial cirri; *PdGngI*, *PdGngVIII*, podial ganglia of first and eighth somites; *PdNv*, podial nerve; *Perst*, peristomium; *Plp*, palpus; *Prst*, prostomium; *SoeGng*, subesophageal ganglion; *StCon*, stomodaeal nerve connective; *StGng*, stomodaeal ganglion; *Stom*, stomodaeum; *Tl*, tentacle.

Nerves of Nereis (fig. A): *a*, nerve to stomodaeum; *b*, tentacle nerve; *c*, *d*, nerves to muscles and prostomial integument; *e*, nerve to proboscis; *f*, palpus nerve; *g*, tegumentary nerve; *h*, *i*, ocular nerves; *j*, nerve to nuchal organ; *k*, commissural ganglion; *l*, *m*, nerves to proboscis; *n*, connective between peristomial ganglia; *o*, nerve to second peristomial ganglion (podial ganglion, *PdGng*); *p*, nerve to proboscis; *q*, *r*, nerves to muscles and integument of peristomium.

to the same somite, and, furthermore, it sometimes contains the ganglia of more than one somite. In the polychaete family Amphinomidae there is, in addition to the median nerve cords, a pair of lateral cords extending posteriorly from the brain (fig. 17 B, *PdNv*), which unite the series of podial ganglia (*PdGng*) lying at the bases of the parapodia (see Storch, 1912, 1913, Gustafson, 1930). The tetra-neurous structure is regarded by Storch as representing the more primitive condition of the annelid nervous system, though Gustafson contends that it is probably secondary. According to a theory proposed by Jeener (1928) the lateral line system represents a primitive series of neuromuscular sensory organs, from which there has been preserved and developed in the Sedentaria the sensorial elements, in the Errantia the ganglionic elements, and in the Oligochaeta the muscular elements.

The annelid brain in its simplest form probably consists of a homogeneous mass of neurocytes aggregated upon a fibrous commissure continuous on each side with the stomodaeal connectives, and through the latter with the ventral nerve cords (fig. 19 A, B, *Br*). With higher development, however, specialized groups of cells appear in the cortex, and specific tracts of fibers are individualized in the neuropile. A very simple brain structure occurs in the archiannelid *Polygordius* (fig. 18 A), in which, according to Hanström (1929), a pair of glomerulous association centers (*PlpGlm*) receive the roots of the palpal nerves and are connected by a palpal commissure (*PlpCom*). The peripheral sense cells of the palpi form ganglionlike masses (*SCIs*) at the bases of the appendages. Two posterior lobes of the brain (*NL*) are connected with the nuchal organs, but eyes and anterior tentacles are absent in *Polygordius*.

In the active polychaetes, in which cephalic tentacles, palpi, eyes, and nuchal organs are well developed, the brain takes on a more complex form and may acquire a high degree of differentiation in its internal organization. Particularly conspicuous are the paired cellular and fibrous masses known as corpora pedunculata. Each of these bodies consists of a cap of small chromatic cells lying in the upper anterior part of the cortex (fig. 18 B, E, *Gb*), and of a stalk, or pedunculus (*Ped*), composed of the neurites of the cap cells, which penetrate the central part of the brain. Within the stalks the terminals of the neurites (*B, d*) form synaptic associations between fibers from all other parts of the brain and from the ventral nerve cords (*a, b, c*). A simple development of the corpora pedunculata is shown by Hanström (1927) to occur in the Hesionidae (fig. 18 D), in which the caps consist each of a single globulus of cells, and the stalks are

connected by a fibrous commissure. In most of the other errant polychaetes the corpora pedunculata are more highly developed, and the cap cells become segregated into two or three distinct globuli (E, F). On the other hand, in the sedentary polychaetes with reduced cephalic

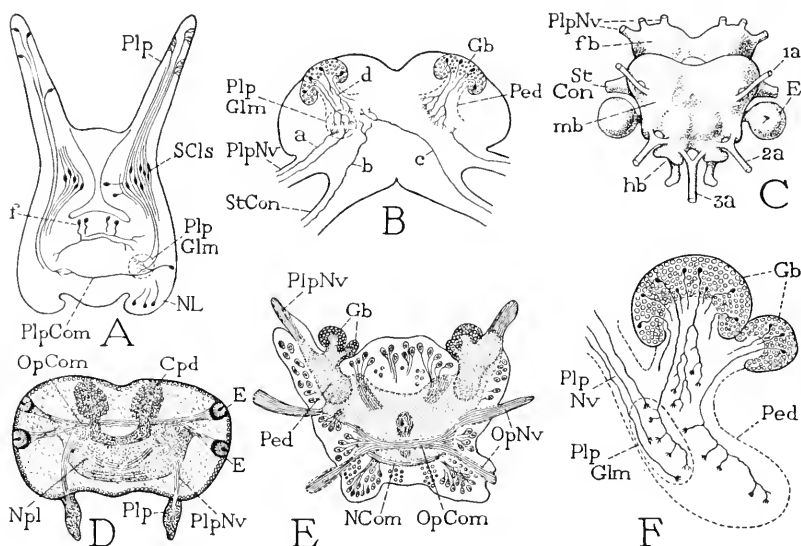


FIG. 18.—Structure of the brain in Archiannelida and Polychaeta.

A, outline of head and diagram of simple brain structure in *Polygordius* (from Hanström, 1929). B, horizontal section of brain of *Sthenelais picta* Verrill (Aphroditidae), diagrammatic (from Hanström, 1927). C, brain of *Eunice punctata* Risso (Eunicidae), showing high degree of external differentiation (from Heider, 1925). D, transverse section of brain of *Podarke obscura* Ehlers (Hesionidae) through corpora pedunculata (from Hanström, 1927). E, horizontal section of brain of *Nereis virens* Sars (Nereidae) showing internal structure (from Hanström, 1927). F, diagram of a corpus pedunculatum of *Nereis virens* (from Hanström, 1927).

a, sensory fibers of palpus nerve; 1a, 2a, 3a, nerves of lateral and median prostomial tentacles; b, c, fibers of stomodaeal connectives; d, axons of globuli cells of corpus pedunculatum; E, eye; f, central neurocytes in anterior part of brain; fb, forebrain; Gb, globulus of corpus pedunculatum; hb, hindbrain; mb, midbrain; NL, nuchal lobe; NCom, nuchal commissure; OpCom, optic commissure; OpNv, optic nerve; Ped, pedunculus of corpus pedunculatum; Plp, palpus; PlpCom, palpal commissure; PlpGlm, palpal glomeruli; PlpNv, palpal nerve; SCls, sense cells of palpus; StCon, stomodaeal connective.

sense organs, the corpora pedunculata are correspondingly reduced or are vestigial, and in the Oligochaeta they are absent.

The development of the corpora pedunculata in the Polychaeta is clearly correlated with the development of the prostomial sense organs, but the particular relationships of the bodies are with the sensory nerves of the palpi. It is shown by Hanström (1927, 1928, 1929) in

the Hesionidae (fig. 18 D), the Aphroditidae (B), the Nereidae (E, F) and other errant families, that the roots of the palpal nerves are closely associated in glomerulous bodies with the stalks of the corpora pedunculata, which fact, Hanström points out, clearly suggests that the corpora pedunculata had their inception as association centers for the sensory nerves of the palpi. Much importance attaches to a study of the corpora pedunculata in connection with annelid and arthropod phylogeny, because bodies very similar in position, structure, and variations are characteristic features also of the brain of Onychophora and Arthropoda.

The relative positions of the principal internal structures of the polychaete brain, it should be noted for later comparison with the onychophoran and arthropod brain, are as follows: Anteriorly and dorsally are the corpora pedunculata (fig. 18 B, D, E); closely associated with the stalks of the latter are the palpal glomeruli (A, B, F, *PlpGlm*), and the glomeruli are connected by a palpal commissure; behind the corpora pedunculata is the optic commissure (D, E, *OpCom*); and in the posterior part of the brain are the nerve centers of the nuchal organs and a nuchal commissure (E, *NCom*). The stomodaeal connectives attach to the ventral surface of the brain.

The number of nerves given off from the brain is highly variable according to the development of prostomial sense organs. In *Polygordius* (fig. 18 A) there is but a single pair of cerebral nerves, which innervate the tentaclelike palpi, while in such forms as *Nereis* (fig. 17 A) an elaborate innervation of the prostomial walls, the sense organs, and the stomodaeum proceeds from the brain.

The principal stomodaeal nerves of the Polychaeta arise in some families from the first ganglia of the ventral nerve cords, or from the brain connectives near these ganglia, while in others they come from the upper parts of the connectives or from the back of the brain. It is contended by Hanström (1927, 1928), therefore, that in the second case the primitive first ganglia of the cords have been drawn forward and united with the brain, forming thus in certain polychaete families a posterior part of the definitive brain corresponding with the tritocerebral lobes of the arthropod brain, which always have connections at least with the stomodaeal (stomatogastric) system of nerves.

The stomodaeal innervation of the Polychaeta is most elaborate in those forms that have a large and eversible stomodaeal proboscis, and in such cases the innervation of the organ may be derived from so many sources that the evidence adduced in favor of Hanström's theory is not convincing. In *Nereis*, for example, Hamaker (1898) describes

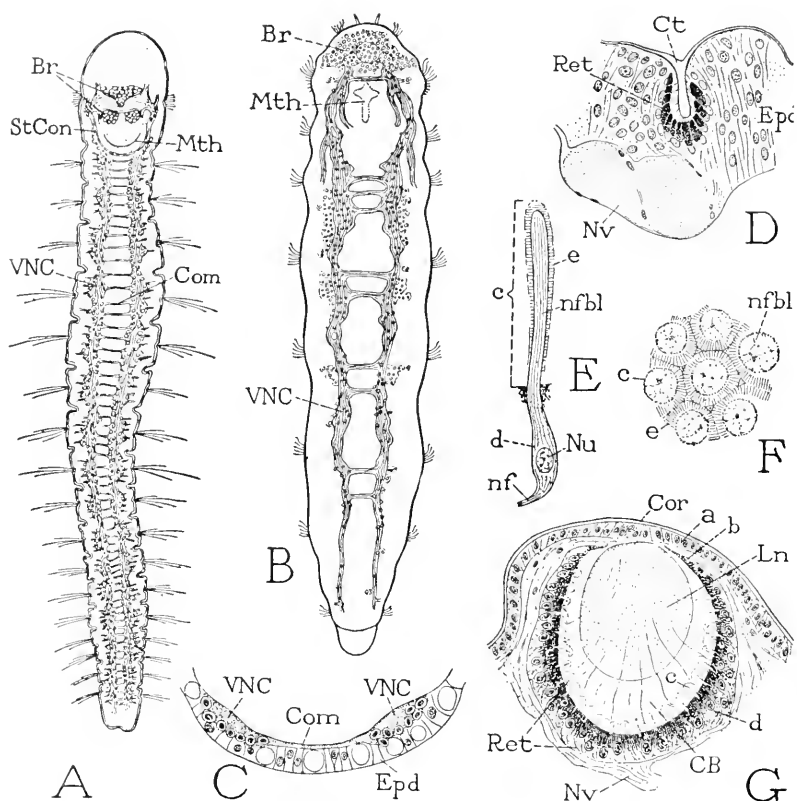


FIG 19.—Examples of generalized structure in the annelid nervous system, and the structure of the annelid eye.

A, the "rope-ladder" type of nervous system in an oligochaete, *Aeolosoma tenebrarum* (from Brace, 1901). B, same in an archannelid, *Dinophilus conklini* Nelson (from Nelson, 1907). C, cross-section of ventral body wall of *Aeolosoma tenebrarum*, showing nerve cords not separated from epidermis (from Brace, 1901). D, vertical section of an eye of primitive structure in a chaetopterid, *Ranzania sagittaria* Claparède (from Hesse, 1899). E, diagram of a typical annelid retinal cell (based on Pflugfelder, 1932). F, cross-section of optic rods of retina of *Heteronereis* sp. (from Pflugfelder, 1932). G, vertical section of eye of a nereid, *Lycastis* sp. (from Pflugfelder, 1932).

a, outer layer of epidermis over eye; b, inner layer of epidermis forming ocular vesicle (see fig. 28 C, D, E); Br, brain; c, optic rod of sensory retinal cell; CB, crystalline body; Com, nerve commissure; Cor, cornea; Ct, cuticle; d, cell body of sensory retinal cell; e, striated border of retinal optic rod; Epd, epidermis; Ln, lens; Mth, mouth; nf, nerve fiber; nfbl, neurofibrillae; Nu, nucleus; Nv, nerve trunk; Ret, retina (including sensory and supporting cells); StCon, stomodaeal connective; VNC, ventral nerve cord.

five pairs of stomodaeal nerves, two pairs of which proceed from the anterior part of the brain (fig. 17 A, *a*, *c*), a third pair (*l*) from small ganglia on the upper ends of the stomodaeal connectives, a fourth (*m*) from the ganglia of the first peristomial cirri, and a fifth (*p*) from the suboesophageal ganglion. In the earthworm, *Lumbricus*, the stomodaeal innervation arises from the connectives between the brain and the first ganglia of the cords (fig. 17 C, *StGng*). Other examples would only show further inconsistencies in the origin of the nerves that supply the annelid stomodaeum. We can, therefore, most readily agree with Gustafson (1930), who concludes that no homology exists between the stomodaeal nervous system of the Annelida and that of the Arthropoda. Gustafson points out, furthermore, in reference to Hanström's theory of transposed ganglia, that there is no concrete evidence of the transfer of a pair of ventral ganglia to the brain in any of the annelids, whereas in the arthropods there is conclusive proof that the tritocerebral ganglia have been secondarily united with the brain. In the higher arthropods, moreover, the ganglia of the stomodaeal nervous system are derived directly from the ectodermal wall of the stomodaeum itself, and their definitive nerve connections with the central system appear to be secondary.

THE EYES

Light-receptive organs in the form of eyes are widely present in the Polychaeta. The polychaete type of eye is fundamentally a vesicular ingrowth of the integument (fig. 28 C, D, E), the retinal cells being epithelial cells of the vesicle wall converted into primary sense cells by the extension of their inner ends as nerve fibers. In the simpler forms of eyes the cuticula may form a mere plug in the cavity of the retinal sac (fig. 19 D), but usually the ingrown part of the cuticula is enlarged and becomes a lenslike body, either connected with the surface by a cuticular strand, or entirely shut in by the union of the lips of the retinal sac (G, *Ln*). The outer ends of the retinal cells form optic rods, converging upon the inner surface of the lens (E, G, *c*), which contain the distal parts of the neural fibrillae (E, *nfbl*), but the apposed surfaces of adjacent rods do not form rhabdoms (F), as they do in the Arthropoda.

THE NEPHRIDIA AND THE GENITAL DUCTS

The most primitive excretory organs of the annelids are the *protonephridia* of trochophore larvae. These are minute tubes, one or two pairs, extending from the body wall into the haemocoel, where they

end blindly, but may be branched; each tube or each branch terminates with a cell that sends a long vibratile flagellum into the lumen of the tube. The larval protonephridia are apparently of ectodermal origin, being said to be formed from primary nephroblasts derived from cells of the third quartet of blastomeres; their structure is essentially that of the "flame cell" tubes of the excretory canals of the Platyhelminthes. Since the larval nephridia are present before the coelomic sacs are formed, they lie within the primary body cavity, which later becomes the haemocoel.

A type of closed nephridium resembling the larval nephridia, and therefore often called a protonephridium, occurs in the five pregenital somites of the archiannelid *Dinophilus* (fig. 13 A), and in the post-larval somites of several families of Polychaeta. The closed nephridia of the adult worm, however, are more highly developed excretory structures than the larval organs, and usually have a more complex end apparatus of tube-cells (solenocytes), which contain long filaments resembling the flagella of the larval nephridia, but said to be nonmotile. The nephridial canal has a simple structure, and its lumen is ciliated. These nephridia project into the coelomic cavities, but, inasmuch as they are ensheathed in folds of the peritoneum, they lie morphologically in the haemocoel. Because of the similarity of their structure to that of the larval nephridia, the closed nephridia of the adult are supposed also to be of ectodermal origin, but their development apparently has not been studied.

The usual adult excretory organ, occurring in most Archiannelida and Polychaeta, and in all Oligochaeta, is of the type called a *metanephridium*. The characteristic feature of a metanephridium is the presence of an inner opening, or nephrostome, by which the nephridial canal communicates with the coelom. Solenocytes in this case are absent. The nephrostome may be a simple ciliated aperture, as in the archiannelids, but more commonly it has the form of a wide, open, ciliated funnel. Unless coelomic dissepiments are absent, the nephrostome always lies in the anterior lamella of the dissepiment before the somite in which the canal opens to the exterior. The canal thus appears to traverse the coelomic cavity behind the funnel, but morphologically it is extracoelomic, since it is ensheathed in a peritoneal fold produced from the posterior lamella of the dissepiment bearing its funnel. A closed nephridium is without doubt strictly an excretory organ, but an open nephridium may serve both for the removal of excretory products and for the discharge of the gametes from the coelom.

The reproductive elements of the annelids are liberated in various ways. In some of the Archiannelida and Polychaeta there is no anatomical provision for the discharge of the sex products from the coelomic sacs, and in such cases the gametes escape by a rupture of the body wall or by fission of the rear part of the body. With certain polychaetes having closed nephridia, a funnel-shaped structure is developed in the genital somites on the anterior surface of the septum, which at maturity opens into the canal of the nephridium, and serves as an outlet for the gametes; but again in others the funnel, though present, is a mere "ciliated organ" of the coelomic peritoneum, not known to acquire an opening. Special genital ducts with an internal funnel and an external aperture are present in only a few Polychaeta, as in some of the Capitellidae, but they are characteristic features of the genital segments of Oligochaeta and Hirudinea. In most of the Polychaeta the nephridial funnels serve for the discharge of the gametes.

The relationship of the various types of annelid excretory organs and genital ducts to one another is difficult to understand. According to the well-known theory of Goodrich (1898-1900), nephridia and genital ducts, or coelomoducts, originally formed two separate series of segmental organs, and are still retained as such in Oligochaeta, Hirudinea, and certain Capitellidae. In the majority of the Polychaeta, however, Goodrich claimed, the genital funnel has lost its own duct and its funnel has united with the mouth of the nephridium, intermediate stages being suggested in some forms where there is a partial fusion between the funnel and the nephrostome.

The study of the development of the open nephridia has given rise to much difference of opinion as to the origin of the nephridial rudiments. The earlier investigators, such as Hatschek and Vejdovsky, regarded the nephridial funnels and canals as mesodermal structures, but Whitman (1886) claimed that the nephridia of the leech *Clepsine* are entirely of ectodermal origin. Wilson (1889), in his work on the development of *Lumbricus*, described the nephridial canals as being apparently ectodermal structures, developed from continuous rudiments formed from the second and third rows of ectodermal cells of the germ band, though he admitted they might be mesodermal; the funnels, however, he said are derived separately from the anterior walls of the coelomic septa. Staff (1910) asserted also that the nephridial canals are ectodermal products in *Criodrilus*, but are formed from only the second row of cells in the germ band; and Tannreuther (1915) claimed the nephridia of *Bdellodrilus* have the same origin, though he did not follow their complete development.

On the contrary, nearly all other investigators have stoutly maintained that both the funnels and the canals are mesodermal, though some regard these two parts as derived from separate rudiments. In this class may be mentioned E. Meyer (1887, *Psygnobranchius*), Bergh (1888, *Criodrilus*, 1890, *Lumbricus*, 1899, *Rhynchelmis*), Bürger (1891, *Nephelis*, 1894, *Hirudo*, *Aulastomum*), Michel (1898, *Allolobophora*), Lillie (1906, *Arenicola*), Bychowsky (1921, *Clepsine*), Penners (1924, *Tubifex*), and A. Meyer (1929, *Tubifex*). Only Bergh is insistent that the entire nephridium is mesodermal; most of the others admit that a terminal part, perhaps including the reservoir, may be formed from the ectoderm.

According to Lillie, the nephridia of the polychaete *Arenicola cristata* are gradually differentiated in the somatic mesoderm, starting from the posterior angles between the septa and the body wall, but the mesoderm in early stages of somite formation presents no cell boundaries. The lumen of each organ appears as a minute intracellular canal, which from its inception opens through the dissepiment into the preceding coelomic cavity. Later, as the nephridial cells divide, the lumen becomes intercellular, and finally it opens posteriorly through the ectoderm. Lillie says, however, that there is no invagination of the ectoderm, and no specific evidence that the reservoir is an ectodermal formation.

Those writers who claim that the nephridia of the Oligochaeta and Hirudinea are of mesodermal origin agree essentially with Bergh that each organ is formed from a single cell of the anterior lamella of an intersegmental septum. According to A. Meyer (1929), for example, the nephridioblasts of *Tubifex* are early differentiated from the other cells of the septa by their large size (fig. 20 A, *Npbl*). By successive divisions of the nephridioblast a column of cells is formed that pushes backward within a sheath of ordinary epithelial cells derived from the posterior lamella of the septum (B-E). The young nephridium extends in a space between the somatopleure and the longitudinal muscles, and is thus *extracoelomic*. The lumen appears first as an intracellular canal, which later becomes intercellular by a radial division of the cells; it is ciliated from an early stage. Posteriorly the canal ends against an epidermal cell (G), through which it eventually opens to the exterior, and from which is later generated the reservoir. The coelomic funnel is formed by the original teloblast, the nucleus of which divides into four nuclei, one taking a position in the dorsal lip of the funnel, the other three in the ventral lip (H, I). According to Bergh (1899) only the lower lip of the funnel in *Rhynchelmis* is derived from the nephridioblast, the upper

lip being formed from a neighboring group of septal cells. In *Clepsine*, Bychowsky (1921) says, the first division of the nephridioblast is in the plane of the dissepiment, and gives rise to an anterior cell that forms the funnel and the adjacent part of the canal, and a posterior cell that generates the rest of the canal. The latter opens finally to the exterior through an ectodermal invagination. Bergh

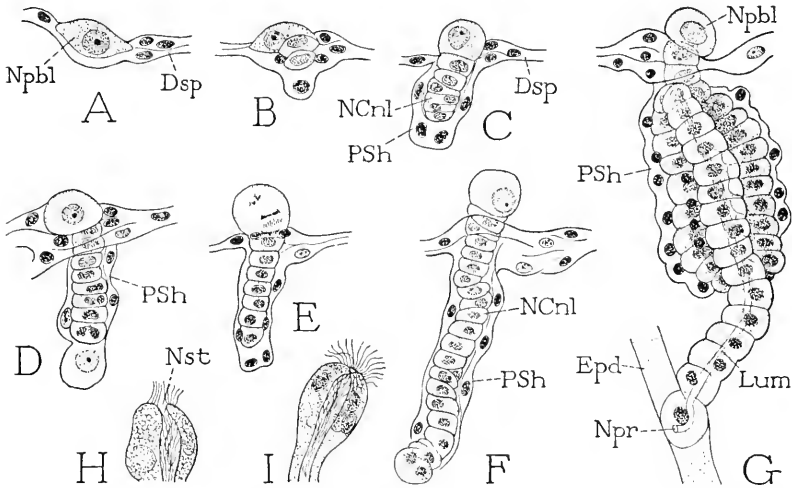


FIG. 20.—Successive early stages in the development of the posterior nephridia of the oligochaete *Tubifex rivulorum* Lam. (From A. Meyer, 1929.)

A, a primary nephridioblast developed from a cell of the anterior lamella of a dissepiment. B, proliferation of nephridial cells by transverse division of the nephridioblast. C-F, successive extensions of the nephridial canal within a peritoneal sheath derived from the posterior lamella of the dissepiment; the canal acquires first an intracellular lumen. G, the canal still more elongate and looped upon itself, attached posteriorly to an epidermal cell, through which the lumen penetrates to the exterior, and which later forms the nephridial bladder. H, I, two stages in the final development of the nephrostome in the primary nephridioblast by radial division of the nucleus.

Dsp, dissepiment; *Lum*, lumen; *NCnl*, nephridial canal; *Npbl*, nephridioblast; *Npr*, nephropore; *Nst*, nephrostome; *PSh*, peritoneal sheath.

claims that there is no ectodermal element in the nephridium of *Criodrilus*, *Rhynchelmis*, or *Lumbricus*.

It thus appears to be now well established that the metanephridia of the annelids in general are structures of the nature of coelomoducts, formed principally as outgrowths of the posterior walls of the coelomic sacs, but perhaps including a terminal part of variable extent derived from the ectoderm. They are extracoelomic, inasmuch as each nephridial canal is invested in a fold of the coelomic peritoneum. The nephridial organs have always been important subjects in dis-

cussions of relationships between the Annelida, the Onychophora, and the Arthropoda. The onychophoran nephridia, however, are developed as simple diverticula of the ventral walls of the coelomic sacs, which connect with short ectodermal ingrowths of the same segments situated mesad of the leg bases, and the nephridial organs of the arthropods most probably have had the same genesis as the onychophoran organs. Hence, it is possible that the coelomic exits have had an independent origin in the higher Annelida on the one hand, and in the common ancestors of the Onychophora and Arthropoda on the other.

V. THE ONYCHOPHORA

Somewhere from a generalized annelid stock there must have branched off in remote pre-Cambrian time the ancestors of the group of animals that includes the modern Onychophora (fig. 21 A), the Cambrian *Aysheaia* (B), and the pre-Cambrian *Xenusion* (C). The primitive onychophorons undoubtedly were segmented, wormlike creatures, in which coelomic sacs and the basic features of the annelid muscular and nervous systems had long been established, and in which the body had been lengthened by the addition of a series of reproductive somites generated from the posterior zone of growth. A distinctive feature of the Protonychophora, however, was the possession of movable locomotor appendages having the form of small lobelike outgrowths of the body wall along the lateroventral lines of the segments. The ancestors of the lobopod Onychophora, and the ancestors of the chaetopod Annelida, therefore, probably constituted two divergent branches from a generalized annelid stock. The primitive chaetopods were creeping worms that progressed by the usual vermiform movements of the body, produced by the body musculature with the aid of integumental chaetae. The primitive onychophorons became distinguished as walking worms, a character well expressed in the name *Peripatus* (Guilding, 1826) given to the first-described modern form. The walking habit led to the adaptation of the modern Onychophora to life on land, but the older forms, such as *Aysheaia* and *Xenusion*, may have been inhabitants of the ocean.

A typical onychophoron is a slender wormlike creature with a pair of tentacular antennae at the anterior end of the trunk, and a double row of short, conical, lateroventral legs along the length of the body (fig. 21 A). The trunk is cylindrical or somewhat depressed, blunt anteriorly, and tapering posteriorly. The rough integument is closely ringed, but there is no external sign of segmentation except for the series of appendages. The animal has no distinct head; the anterior

part of the trunk, however, forms a cephalic lobe (D, E) bearing the antennae, a pair of small dorsal eyes (E, E) just behind the antennal bases, and on the ventral surface the mouth (D). The mouth, which is a triangular opening into the stomodaeum, is sunken into a preoral cavity surrounded by an integumental circumoral fold

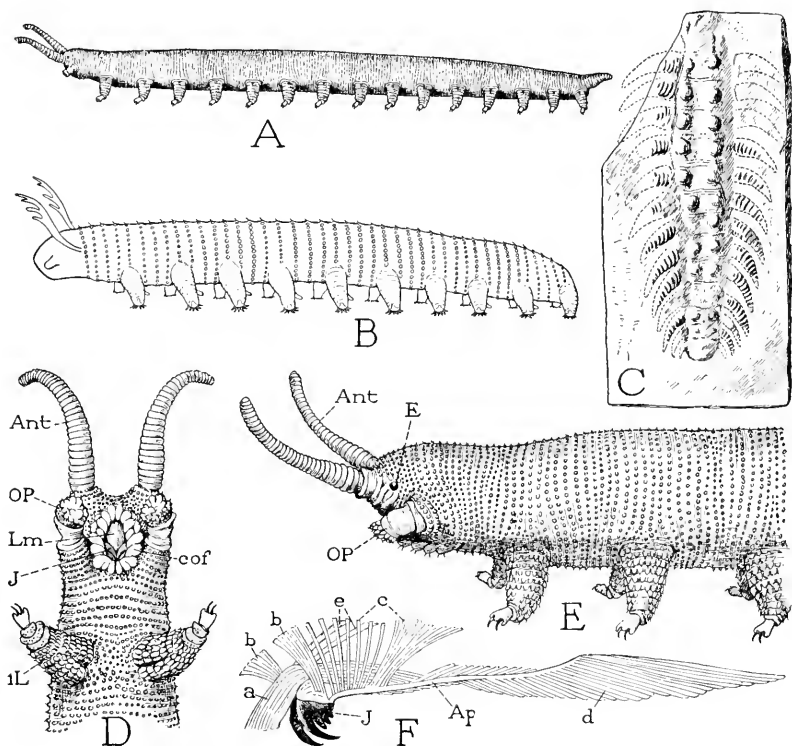


FIG. 21.—Onychophora, ancient and modern.

A, *Peripatoides norae-zelandiae* Hutton. B, *Aysheaia pedunculata* Walcott (1911), of Middle Cambrian, British Columbia, "conjectural restoration" (from Hutchinson, 1930). C, *Xenusion auerswaldi* Pompeckj (1927), of Algonkian, proterozoic pre-Cambrian (from Heymons, 1928, broken lines hypothetically completing lacking parts). D, *Peripatoides norae-zelandiae*, anterior part of trunk, ventral view. E, same, head and anterior part of body, lateral view. F, same, right jaw, dorsal view, with muscles.

a-d, jaw muscles; Ant, antenna; Ap, apodeme of jaw muscles; cof, circumoral fold; E, eye; J, jaw; 1L, first leg; Lm, labrum; OP, oral papilla.

(cof). Within the preoral cavity is a small anterior labral lobe (Lm), and a pair of flat, two-hooked jaws (J) that converge posteriorly at the sides of the mouth. On the sides of the head, laterad of the mouth, is a pair of oral papillae (E, D, Op) that give vent to a pair of large, many-branched slime glands widely spread in the

body cavity (fig. 32 A, *SlmGld*). The following appendages are the legs, varying in number with different species from a minimum of 13 pairs to an average of perhaps 25 or 30 pairs, though some species have 40 or more. Behind the last legs the body tapers to a terminal cone on which is situated the anus. The genital aperture in each sex is a median ventral opening lying either between the legs of the last pair, or behind the last pair present in species having one or two of the posterior pairs of legs absent.

EARLY STAGES OF DEVELOPMENT

Were it not for the evidence of annelid relationships shown in the adult structure of the Onychophora, we should have little reason for believing that the onychophorons are descended from Annelida, for in their ontogeny we encounter none of the familiar early phases of development so characteristic of the annelids. Most of the Onychophora are viviparous, the embryos developing to maturity in uterine chambers of the oviducts (fig. 32 A, *Utrs*); only a few species are known to be oviparous. Eggs supplied with a large quantity of deutoplasm complete their development from their own store of yolk, but the embryos of viviparous species with small eggs receive nourishment from the uterine walls, and in some cases a placentalike growth of the blastoderm forms a large vesicular trophoblast applied to the walls of the uterus.

The early stages of onychophoran development are so variable in different species that it is impossible to give any general account of the processes of cleavage and germ-layer formation. Cleavage in some species with small eggs is holoblastic, producing first a solid morula and then a hollow blastula (see Sclater, 1888). Contrary to what we might expect, however, gastrulation in such cases does not take place by invagination. In *Peripatus imthurni*, as described by Sclater, an internal proliferation of cells proceeds from a definite point on the blastula, and the cells thus produced become differentiated into endoderm and mesoderm. A similar method of endoderm-mesoderm formation is described by Kennel (1888) in *Peripatus edwardsi*, there being here a blastoporic depression of the blastoderm from which an internal proliferation gives rise to endoderm and to ventrolateral bands of mesoderm. With eggs having much yolk, meroblastic cleavage is the rule. The egg nucleus divides within the yolk, and the cleavage nuclei enclosed in small masses of cytoplasm migrate to the surface and form a blastoderm. In *Peripatoides novae-zealandiae*, however, according to Sheldon (1888), the blastoderm

lies beneath a superficial layer of yolk, the early embryo in this case being a sac not only containing yolk, but also surrounded by it. The outer yolk is later absorbed. In this species the manner of germ-layer formation has not been definitely determined, but the endoderm cells appear within the yolk, and the mesoderm takes the form of two widely separated bands along the sides of the embryo, in which the coelomic sacs are formed.

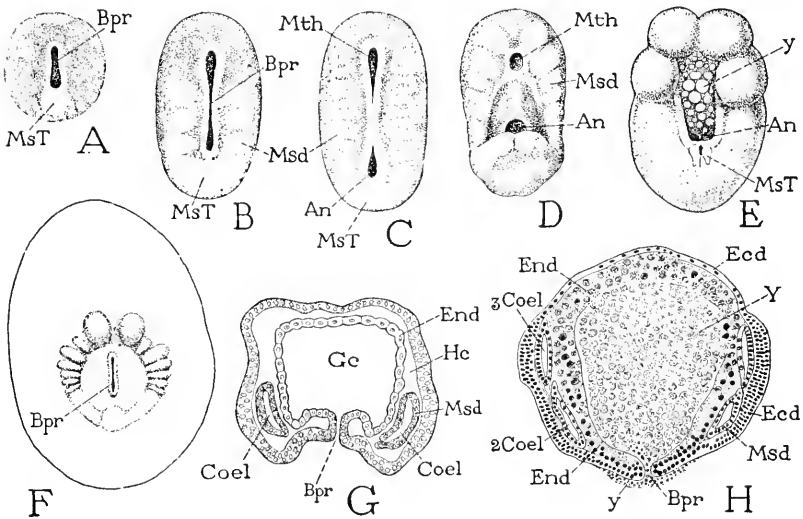


FIG. 22.—Early developmental stages of Onychophora.

A-D, successive embryonic stages of *Peripatopsis capensis* Grube, showing elongation and closure of the blastopore except at oral and anal extremities, and forward growth and segmentation of mesoderm bands (from Balfour, 1883). E, young embryo of *Eoperipatus weldoni* Evans, ventral view, mouth covered by external yolk (from Evans, 1902). F, young embryo of *Peripatopsis moseleyi* Wood-Mason with open blastopore (from Bouvier, 1905). G, cross-section of embryo of *Peripatopsis capensis* through open blastopore (from Balfour, 1883). H, cross-section of embryo of *Eoperipatus weldoni*, blastopore covered with yolk (from Evans, 1902).

An, anus; Bpr, blastopore; Coel, coelomic cavity; 2Coel, 3Coel, second and third coelomic cavities; Ecd, ectoderm; End, endoderm; Gc, gastrocoele; Hc, haemocoel; Msd, mesoderm; MsT, mesodermal teloblast ("primitive streak"); Mth, mouth; Y, internal yolk; y, external yolk.

In *Peripatopsis capensis*, Sedgwick (1885) says, cleavage is complete but unequal, the blastomeres being differentiated into four small, dark ectodermal cells at the animal pole of the egg, and four large, clear endodermal cells at the vegetative pole. Subsequent divisions proceed in each group separately. The endoderm cells soon draw together into the center of the egg, and are here overgrown by the ectoderm until completely enclosed by the latter, except at one point where

the endoderm remains exposed on the surface. A cavity now appears in the endodermal mass, and opens externally where the endoderm is not covered by the ectoderm. The opening is the blastopore (fig. 22 A, *Bpr*). With the growth of the embryo, the blastopore lengthens to an elongate slit on the ventral surface (B). The first observations on the development of *Peripatopsis capensis* were made by Balfour (1883), who believed that the mesoderm arises in the form of paired coelomic pouches along the edges of the elongate blastopore where the ectoderm and endoderm are confluent. From the subsequent work of Sedgwick, however, it appears that the mesoderm in *P. capensis* is generated from an opaque area of the blastoderm situated behind the posterior end of the blastopore (A, B, C, *Mst*). From this area, or "primitive streak," there takes place an internal proliferation of cells, which, migrating forward in each side of the embryo, produce two ventrolateral mesoderm bands along the margins of the blastopore (B). The bands then break up into sections that mark the primitive somites of the embryo, and later are excavated by the coelomic cavities (G, *Coel*). The elongate blastopore finally closes by the fusion of its lips, except at the two ends, which become the primary mouth and the primary anus (D, *Mth*, *An*).

The development of the endoderm of *Eoperipatus weldoni*, as described by Evans (1902), is again different from that of *Peripatopsis capensis*. "The endodermal elements," Evans says, "are derived from the lips of the blastopore and travel inward along the outer layers of the yolk, which is at first devoid of nuclei." Here, evidently, is a process suggesting invagination. On the surface of the yolk the endoderm cells form a complete investing layer, but later some of them invade the yolk, probably bringing about its partial digestion, and then again most of these cells return to the surface, where they reconstruct a permanent endodermal sac containing the yolk (fig. 22 H, *End*). A few endodermal cells, however, remain within the yolk. The mesoderm of *Eoperipatus weldoni*, according to Evans, is formed in the same way as described by Sedgwick for *Peripatopsis capensis*, that is, from a proliferating area of the blastoderm situated immediately behind the blastopore (E, *Mst*).

Considering the various processes by which the organization of the onychophoron is accomplished in the embryo, it would appear that the manner of development has little significance. In extreme cases the assembling of the germ layers seems to be almost haphazard. Sheldon (1888) observes of *Peripatoides novae-zealandiae* that the embryo might be said to be formed "by a process of crystallizing out *in situ* from a mass of yolk, which is a protoplasmic reticulum con-

taining nuclei." Among the early developmental phases of the Onychophora, however, we cannot fail to note two important likenesses to annelid development. The first is the elongation of the blastopore on the ventral surface of the embryo as it occurs in *Peripatopsis capensis* (fig. 22 A, B), followed by the closure of its median part (C), finally leaving only the persistent oral and anal apertures at the two extremities (D). We have here evidently a condition even more generalized than in the annelids, in which the anus is usually a secondary perforation. The second suggestion of annelid development, shown in several onychophoran species, is the forward growth of the mesoderm as bands of cells generated from a proliferating area of the blastoderm situated behind the blastopore (fig. 22 A, B, C, E, *MsT*). The mesoderm is, therefore, a teloblastic product, though it is not possible to identify in the generative area a primary pair of teloblastomeres. It would appear, however, that the onychophoran mesoderm may not be entirely of teloblastic origin, for Sedgwick (1887) finds that the forwardly growing bands in *Peripatopsis capensis* are augmented by cells proliferated from the lips of the blastopore along the lines where ectoderm and endoderm meet. The later development of the mesoderm is unquestionably a strictly homologous process in both the Annelida and the Onychophora, for in the latter, as in the annelids, the primarily solid mesoderm bands are first segmented corresponding with the body somites (fig. 22 B), and then excavated by coelomic cavities (C, G).

Beyond the early stages of cleavage and germ-layer formation the course of onychophoran ontogeny is well standardized and gives a good basis for comparison of the Onychophora with the Annelida on the one hand, and with the Arthropoda on the other. It will be found, however, that many of the irregular earlier processes of onychophoran development are duplicated among the Arthropoda.

THE NERVOUS SYSTEM

The onychophoran nervous system includes a brain situated in the head above and before the decurved anterior end of the stomodaeum (fig. 32 A, *Br*), and two long, widely separated nerve cords (*NC*) extending from the brain to the posterior end of the body, where they appear to be continuous in an arc above the rectum. The cords are connected by numerous ventral commissures (*Com*), and they give off in each segment a series of dorsal nerves against the body wall (fig. 24 B) and ventral nerves that go downward to the legs and other ventral parts. Opposite the legs the nerve cords are slightly

thickened, but they have no differentiated ganglia, since the neurocytes are scattered along their lengths. The brain, on the other hand, is a well-developed, bilobed cerebral body (fig. 25 A, B) extending horizontally forward from the anterior ends of the nerve cords (C). It bears anteriorly the large antennal nerves (*AntNv*), laterally a pair of small optic lobes supporting the eyes (*E*), and ventrally a pair of small pear-shaped bodies (B. C. *1VO*). Numerous other

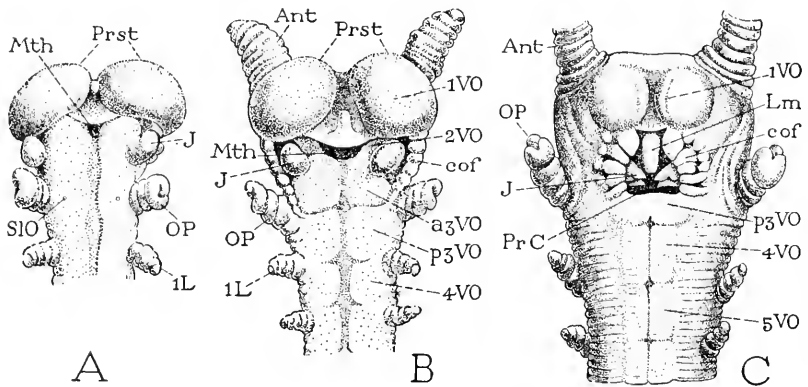


FIG. 23.—Development of the onychophoran head and anterior body region as shown in three embryonic stages of *Peripatus edwardsi* Blanchard, ventral view. (From Kennel, 1888.)

A, young embryo with large prostomial cephalic lobes, postoral jaw appendages (*J*) and oral papillae (*OP*) resembling legs. B, older embryo with prostomial antennal rudiments, jaws approaching mouth and surrounded by circumoral fold (*cof*), ventral organs (*VO*) becoming differentiated. C, still older embryo; jaws with definitive form, retracted into preoral cavity, ventral organs more distinct; head region composed of procephalic lobes, jaw somite, and somite of oral papillae.

a3VO, anterior ventral organ of papillar somite; *cof*, circumoral fold; *J*, jaw; *L*, leg; *Lm*, labrum; *Mth*, mouth; *OP*, oral papilla; *PrC*, preoral mouth cavity; *Prst*, prostomium; *p3VO*, posterior ventral organ of papillar somite; *SIO*, orifice of salivary gland; *1VO*, ventral organ of preoral cephalic lobe; *2VO*, ventral organ of jaw somite; *3VO*, ventral organ of somite of oral papillae (subdivided into anterior and posterior parts); *4VO*, *5VO*, ventral organs of first and second leg somites.

small nerves are given off from the brain (fig. 24 A), among which are anterior ventral nerves that go to the mouth and the circumoral fold, a dorsal median nerve (*f*) that turns downward and posteriorly on the dorsal surface of the stomodaeum, a pair of posterior stomodaeal nerves (*i*), and the nerves of the jaws (*j*), which arise from the nerve cords just behind the brain.

The entire central nervous system of the Onychophora is developed in the embryo from a series of paired ventral thickenings of the ectoderm known as the "ventral organs" (fig. 23 B, C, *VO*), which

correspond with the embryonic somites, except that the first pair (*IVO*) lies on the preoral head region. Whether these thickenings represent primitive organs or are merely embryonic structures is open to question, but they suggest the paired tubercles on what may be the ventral surface of *Xenusion* (fig. 21 C). From the inner surfaces of the ventral organs of the body are differentiated the

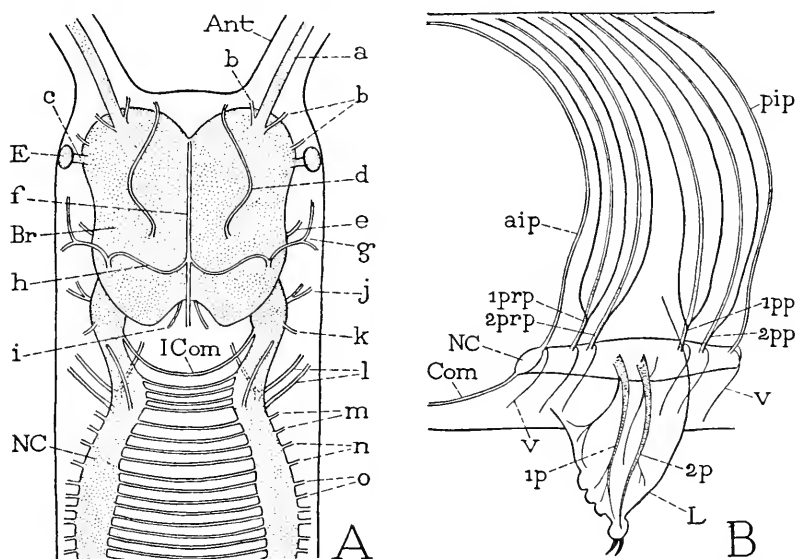


FIG. 24.—Nervous system of the head and of a body segment of *Peripatus tholloni* Bouvier. (From Fedorow, 1926, 1929.)

A, diagram of brain and anterior parts of nerve cords, with bases of nerves, dorsal view. B, nerve cord and peripheral nerves of left side of a body segment, lateral view.

a, sensory antennal nerve; *aip*, anterior interpedal nerve; *Ant*, antenna; *b*, motor nerves of antenna; *Br*, brain; *c*, optic nerve; *Com*, nerve commissure; *d*, lateral dorsal nerve; *E*, eye; *e*, nerve to circumoral fold; *f*, median dorsal nerve; *g*, nerve to dorsal muscles of head; *h*, commissural nerve from *f* to *g*; *i*, stomodaeal nerve; *ICom*, first ventral commissure; *j*, *k*, nerves of jaw; *L*, leg; *l*, nerves of oral papilla; *m*, *n*, *o*, nerves of first leg segment; *1p*, *2p*, first and second pedal nerves; *1pp*, *2pp*, first and second postpedal nerves; *pip*, posterior interpedal nerve; *1prp*, *2prp*, first and second prepedal nerves; *v*, ventral nerves.

ventral nerve cords; the outer parts are then gradually reduced in size until finally they disappear as distinct areas of the epidermis. When the nerve strands become free cords within the body they do not approach each other or unite as do the nerve cords of most annelids or arthropods; on the contrary they *move farther apart* until they take positions along the sides of the body on a level with the leg bases (fig. 29, *NC*). The definitive cords, moreover, lie laterad of

series of dorsoventral lateral muscles (*dvm*) attached dorsally and ventrally on the body wall. A condition thus arises in the Onychophora that has no counterpart in the annelids or arthropods, for in the latter the nerve cords, even when laterally situated, have no barrier to a median approximation or union.

The major part of the brain, from which arise the antennal and optic nerves, is shown by Sedgwick (1888), Kennel (1888), and Evans (1902) to be generated from the paired ventral organs of

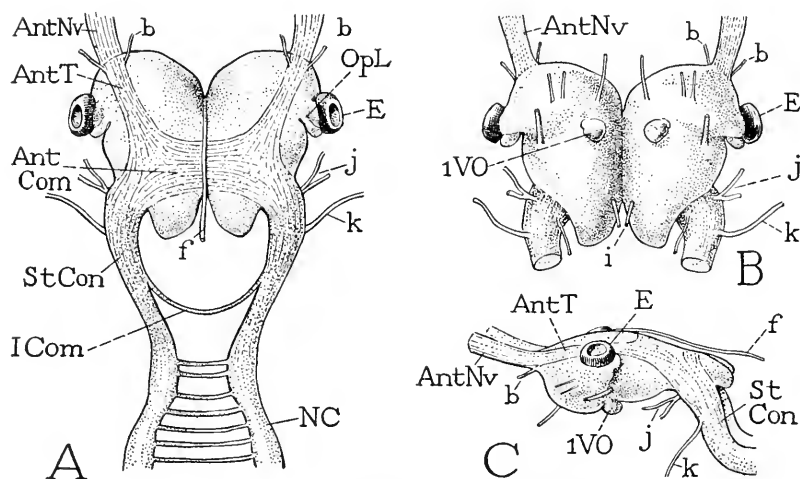


FIG. 25.—Brain of *Peripatoides novae-zealandiae* Hutton.

A, dorsal surface of brain and anterior parts of nerve cords, showing posterior antennal commissure and dorsal position of antennal tracts. B, ventral surface of brain, with remnants of ventral organs. C, lateral view of brain and stomodaeal connectives.

AntCom, antennal commissure; *AntNv*, antennal nerve; *AntT*, antennal tract; *b*, motor nerves of antenna; *E*, eye; *f*, median dorsal nerve; *i*, stomodaeal nerves; *ICom*, first ventral commissure; *j*, *k*, nerves of jaw; *NC*, nerve cord; *OpL*, optic lobe; *StCon*, stomodaeal connective; *1VO*, remnant of first ventral organ.

the head (figs. 23 B, 27 B, *1VO*). Evans says that the brain includes also a pair of anterior "archicerebral lobes" belonging to the apical part of the head, but in his account of the embryonic development of *Eoperipatus weldoni* he makes no mention of observing a separate origin of such lobes, and attributes the entire brain, except a posterior part, to the neural elements derived from the cephalic ventral organs. The ventral organs of the head, unlike those of the body, are finally invaginated as vesicles connected with the nerve tissue; eventually they are reduced, but persist as the small bodies attached to the ventral side of the brain (fig. 25 B, C, *1VO*).

The small posterior lobes of the brain from which arise the posterior stomodaeal nerves (fig. 25 B, *i*), together with the adjoining parts of the nerve cords that give off the nerves of the jaws (A, B, C, *j*), are said by Evans to be secondarily added to the antenno-ocular lobes from the ventral organs of the postoral jaw somite (fig. 23 B, *2VO*), and Kennel clearly shows in a head section (fig. 27 A) the inclusion in the brain of a mass of neural cells given off from these generative centers (*2VO*). The definitive onychophoran brain, therefore, as

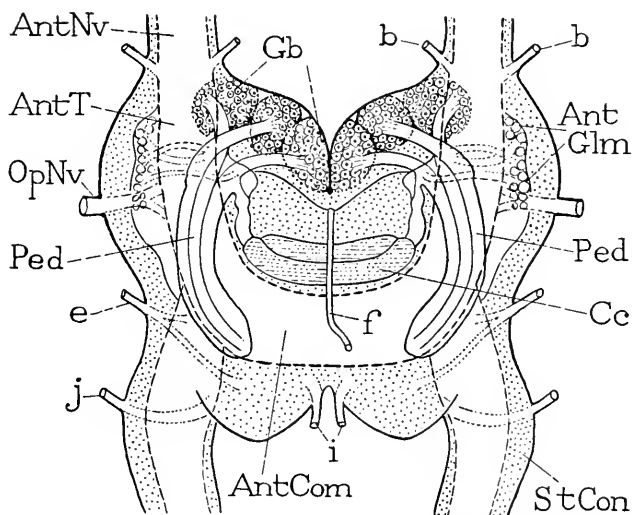


FIG. 26.—Internal structure of the brain of *Peripatopsis capensis* Grube. (From Holmgren, 1916.)

AntCom, antennal commissure; *AntGlm*, antennal glomeruli; *AntNv*, sensory antennal nerve; *AntT*, antennal tract; *b*, motor nerves of antenna; *Cc*, corpus centrale; *e*, nerve to circumoral fold; *f*, median dorsal nerve; *Gb*, globuli of corpus pedunculatum; *i*, stomodaeal nerves; *j*, nerve of jaw; *OpNv*, optic nerve; *Ped*, peduncle of corpus pedunculatum; *StCon*, stomodaeal connective.

shown by the records of its development, and as claimed by Holmgren (1916) and by Hanström (1928, 1935) from histological evidence, would appear to be a syncerebrum composed of a prostomial fore-brain including the ocular and antennal centers, and of a postoral hindbrain containing the centers of the posterior stomodaeal nerves and the nerves of the jaw appendages.

A quite different concept of the composition of the onychophoran brain is deduced by Fedorow (1929) from a study of *Peripatus tholloni*, in which he attempts to correlate the cerebral nerves with the nerves of a series of body segments (fig. 24 A, B). Fedorow

concludes that the anterior part of the brain, lying before the antennal commissure and bearing the optic lobes, represents the prostomial archicerebrum of the annelids, and that the rest of the brain is of postoral origin, being formed of the united anterior ends of the nerve cords extended secondarily in front of the stomodaeum. This alleged postoral part of the definitive brain, Fedorow believes, includes the ganglionic centers of the antennal somite, and the ganglia of a reduced premandibular somite that has lost its appendages. The jaw centers, he contends, are contained in the parts of the nerve cords immediately behind the brain, from which arise the nerves of the jaw muscles (*j*), and which are connected by the first postoral commissure (*1Com*). Fedorow's elaborate analysis of the brain structure and nerves would be more convincing if it took into account the embryonic development of the brain; his results are entirely unsupported by ontogenetic evidence, and are mostly at variance with observations on the brain development reported by other investigators.

The internal structure of the onychophoran brain (fig. 26) shows fundamental characters of the polychaete brain, and contains certain arthropod features, but it presents also special modifications that are not found in either the annelids or the arthropods. Corpora pedunculata are well developed, each consisting of a cap of three globuli (*Gb*) of small chromatic cells lying in the anterior part of the brain, and of a large pedunculus (*Ped*) composed of three confluent groups of fibers springing from the globuli cells. The sensory antennal nerves (*AntNv*) coming into the anterior angles of the brain traverse the upper part of the cerebrum in distinct antennal tracts (*AntT*), which are united posteriorly in a broad antennal commissure (*AntCom*). The association centers of the antennal nerve fibers, called by Holmgren (1916) and Hanström (1928, 1935) the *antennal glomeruli* (*AntGlm*), lie laterad of the anterior ends of the corpora pedunculata, and are said by Hanström to be closely connected with neurites of the globuli cells. In this feature, Hanström points out, the Onychophora have a distinctly polychaete character in the brain structure, since the antennal glomeruli of the onychophoran brain evidently correspond with the palpal glomeruli of the polychaete brain (fig. 18 B, F, *PlpGlm*). On the other hand, the onychophoran brain shows arthropodan characters in the presence of a well-developed central body (*Cc*) and an antennal commissure (*AntCom*). But again, the small optic lobes of the eyes (fig. 25 A, *OpL*) contain each only a single ganglionic center, while all arthropods have at least two. The optic ganglia are connected with the corpora pedunculata and with the central body.

The onychophoran brain thus appears to contain, as Hanström (1935) has shown, a mixture of polychaetous and arthropodan characters. Its origin must be found in the annelid brain; but certain peculiar features of the onychophoran brain would seem to preclude

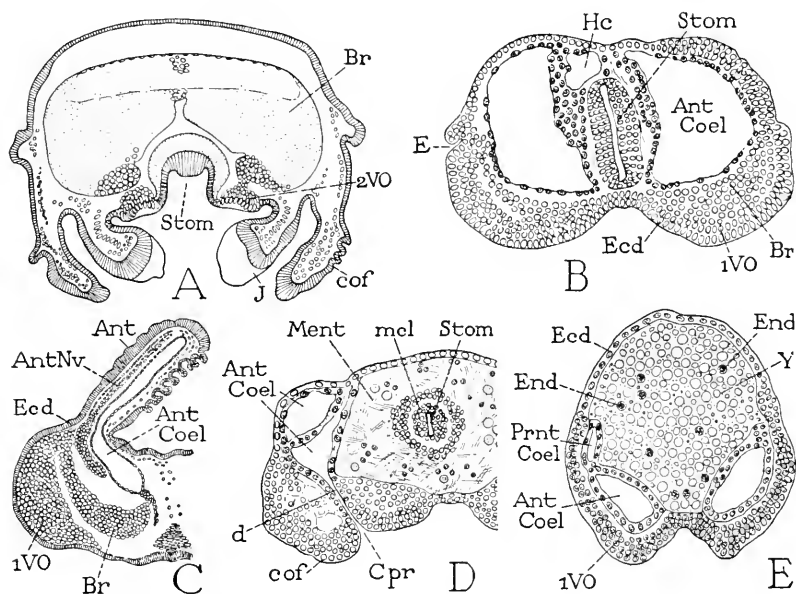


FIG. 27.—Developmental stages of various head structures of Onychophora. (A, C from Kennel, 1888; B, D, E from Evans, 1902.)

A, cross-section of head of embryo of *Peripatus edwardsi* Blanchard through jaws (*J*), showing groups of brain cells proliferated from ventral organs (*2VO*) of jaw somite. B, cross-section of embryonic head of *Eoperipatus weldoni* Evans, showing coelomic sacs of antenna embracing the stomodaeum, and generation of brain (*Br*) from cephalic ventral organs (*1VO*). C, section through anterior part of head of embryo of *Peripatus edwardsi*, showing antennal coelomic sac extending into antenna. D, section of embryonic head of *Eoperipatus weldoni* with canal (*d*) from antennal coelom opening mesad of circumoral fold (*cof*). E, same, more anterior section, showing antennal coelomic sacs, and a pre-antennal sac on left side.

Ant, antenna; *AntCoel*, coelomic sac of antenna; *AntNv*, antennal nerve; *Br*, brain; *cof*, circumoral fold; *Cpr*, coelomopore of antennal coelom; *E*, pit of developing eye; *Ecd*, ectoderm; *End*, endoderm; *Hc*, haemocoele; *J*, jaw; *mcl*, muscles of stomodaeum; *Ment*, mesenteron (folded forward on stomodaeum); *PrntCoel*, preantennal coelom; *Stom*, stomodaeum; *1VO*, preoral cephalic ventral organ; *2VO*, ventral organ of postoral jaw somite; *Y*, yolk.

the possibility of its having given rise to the arthropod brain. The superficial position of the antennal nerve tracts (fig. 25 A, C, *AntT*), which traverse the forebrain *dorsal* to the optic lobes (A, *OpL*), constitutes a condition quite at variance with that in any arthropod, for in all the Arthropoda the antennal nerves issue from antennal lobes

that lie ventral to the optic lobes, showing that the antennae have migrated forward beneath the eyes, and not above them as in the Onychophora. Moreover, in the arthropod brain the antennal glomeruli are not immediately connected with the corpora pedunculata. The onychophoran brain in its modern form, therefore, could not have given rise to a brain of arthropod structure, and we can assume only that the two types of cerebral structure have taken their origins separately from some common progenitor not far removed from a generalized annelid. Even the inclusion of the nerve centers of the first postoral somite in the onychophoran brain cannot be taken as evidence that the Onychophora are ancestral to the Arthropoda, for in some of the lower members of the second group the first postoral (tritocerebral) ganglia are not united with the brain.

THE EYES

The eyes of the Onychophora resemble the eyes of annelids in structure and development. An eye of the annelid-onychophoran type is formed from an invagination of the body wall (fig. 28 C), which becomes closed by an approximation or union of its lips (D, E), thus producing an inner optic vesicle (*OpV*) beneath an outer layer of epidermis and corneal cuticula (*Cor*). The cavity of the vesicle is occupied by a crystalline lens (*Ln*), probably of a cuticular nature, and its inner wall becomes the retina (*Ret*). In the onychophoran eye (A), as described by Dakin (1921), the lens is strongly convex outwardly and rests on the thick retina (*Ret*). Each retinal cell (B) is differentiated into a distal cylindrical rod (*c*) and a basal pigmented part (*d*), which contains the nucleus (*Nu*), and is prolonged proximally as a nerve fiber (*nf*) that enters the optic lobe of the brain. The rods appear to have peripheral striations (*e*), but, as shown in cross-section (F), they do not form structures between them corresponding with the rhabdons of arthropod eyes.

LATER HISTORY OF THE MESODERM AND THE COELOMIC SACS

The mesoderm bands of the Onychophora in their forward growth (fig. 22 B, C) continue into the head, where they form a pair of distinct coelomic sacs in the antennal region diverging anteriorly from the mouth (D). The cephalic coelomic sacs are described by Sedgwick (1887) in *Peripatopsis capensis*, by Kennel (1888) in *Peripatus edwardsi*, and by Evans (1902) in *Eoperipatus weldoni*. The sacs are at first of large size (fig. 27 B); posteriorly their splanchnic walls embrace the stomodaeum (*Stom*) and give rise to a part of the

stomodaeal musculature; anteriorly they extend into the antennae (*C, AntCoel*), and thus show their relation to these appendages. According to Evans, the antennal sacs acquire temporary coelomoducts (*D, d*) opening ventrally to the exterior (*Cpr*) within the circumoral fold (*cof*). With the increase in the size of the brain,

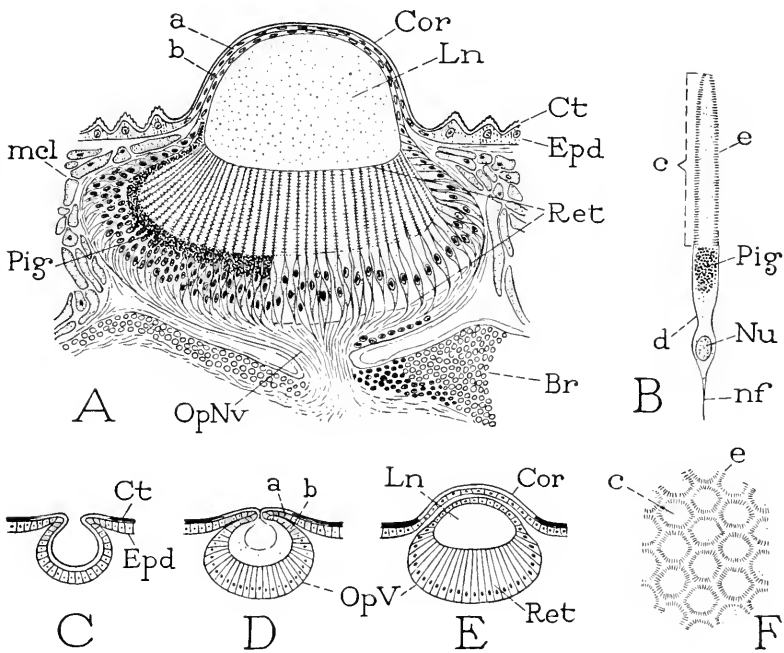


FIG. 28.—Structure of the onychophoran eye. (A, B, F from Dakin, 1921.)

A, vertical longitudinal section of eye of *Peripatoides occidentalis* Fletcher, right half of retina depigmented. B, a retinal cell, differentiated into basal plasmatic part (*d*) and distal optic rod (*c*). C, D, E, diagrams of development of an eye of the vesicular type (see also fig. 19 G). F, tangential section through optic rods of retina.

a, b, outer and inner layers of corneal epidermis; *Br*, brain; *c*, optic rod of retinal cell; *Cor*, cornea; *Ct*, cuticle; *d*, basal plasmatic part of retinal cell; *e*, striated border of optic rod; *Epd*, epidermis; *Ln*, lens; *mcl*, muscle fibers; *nf*, nerve fiber; *Nu*, nucleus; *OpNv*, optic nerve; *OpV*, optic vesicle; *Pig*, pigment; *Ret*, retina.

the antennal sacs become reduced until finally, Evans says, they appear only as two small spaces situated above the brain in front of the eyes.

A pair of small mesoderm masses observed by Evans in an embryo of *Eoperipatus weldoni*, lying above and before the antennal sacs, in one of which a cavity was present (fig. 27 E, *PrntCoel*), are regarded by Evans as representing a pair of preantennal coelomic sacs, possibly

corresponding with a pair of transient rudiments of preantennal appendages mentioned by Kennel in *Peripatus edwardsi*.

The coelomic sacs of the body region conform with the series of postoral somites. The sacs of the jaw somite soon disappear. Those of the following somites attain a high state of development during the early embryonic period, leaving thus no doubt that the Onychophora are descended from typically metameric ancestors. The coelomic cavities become connected with the exterior by ventral diverticula from the mesodermal walls of the sacs (fig. 32 C, *c*) that unite with ectodermal invaginations (*d*), and thus form ducts opening on the mesal aspects of the bases of the legs (D). These outlet ducts of the coelomic sacs (coelomoducts) probably served primarily in the early history of the Onychophora for the discharge of excretory products and the gametes (fig. 34 A); but the coelomic sacs of the somites anterior to the somite of the definitive genital outlets become differentiated into dorsal gonadial and ventral nephridial compartments (B, C, *a*, *b*). The gonadial compartments eventually disappear except in a few posterior segments where they unite to form the gonads; the nephridial compartments are reduced to the form of delicate vesicles at the inner ends of the coelomoducts (D, *b*), and thus persist as end-sacs of the definitive nephridia. In the somite of the genital outlet the entire coelomic sacs (figs. 32 E, 34 E, *a*, *b*) with their coelomoducts (*d*) are converted into the lateral genital ducts. The sacs of the second postoral somite become the salivary glands that open into the preoral mouth cavity. Derivation products of the coelomic walls include the entire muscular system, the dorsal pulsating blood vessel (fig. 29, *DV*), and a muscular dorsal diaphragm (*DDph*) beneath the blood vessel.

THE SOMATIC MUSCULATURE

The body musculature of the Onychophora is in general similar to that of the annelids in so far as it consists mostly of flat sheets or bands of circular, oblique, and longitudinal fibers closely applied to the integument throughout the length of the animal (fig. 29), but it includes a series of lateral dorsoventral fibers (*dvm*) along each side of the body cavity, which have no representatives in annelid musculature. These lateral muscles divide the body cavity into a median compartment (*mBC*) containing the alimentary canal (*AlCnl*) and the slime glands (*SlmGld*), and lateral compartments (*lBC*) enclosing the salivary glands (*SlGld*), the nephridia (*Nph*), and the nerve cords (*NC*). The muscle fibers are all very slender, and for the

most part are not closely grouped into bundles forming specific muscles as in the arthropods. Each fiber is invested in a delicate sarcolemma, the nuclei are superficial, and the axis is distinctly fibrillated but shows no trace of cross striation (see Camerano, 1897).

The following account of the onychophoran body musculature is based on a study of *Peripatoides novae-zealandiae*. When the body is laid open from above there are exposed on each side three sets of

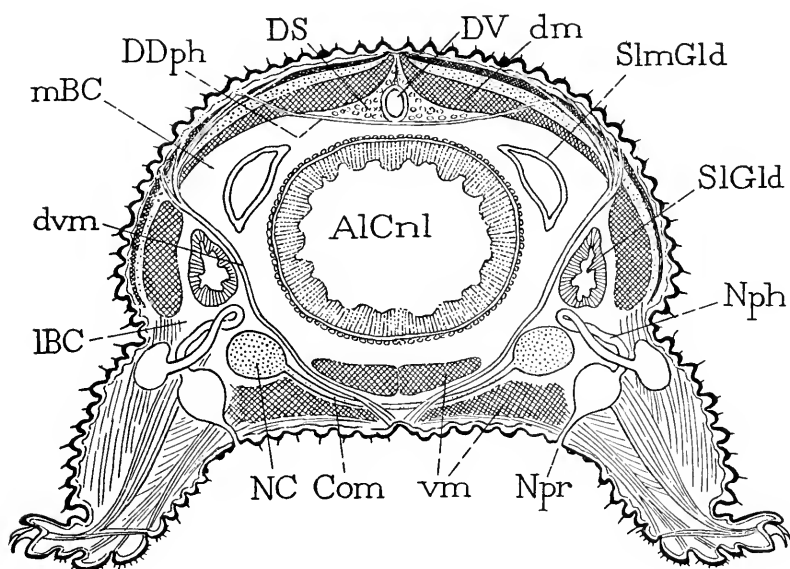


FIG. 29.—Cross-section of middle body region of *Peripatoides novae-zealandiae* Hutton, showing position of principal organs, diagrammatic.

AlCnl, alimentary canal; *Com*, commissure of nerve cords; *DDph*, dorsal diaphragm; *dm*, dorsal muscles; *DS*, dorsal sinus; *DV*, dorsal blood vessel; *dvm*, dorsoventral lateral muscles; *IBC*, lateral compartment of body cavity; *mBC*, median compartment of body cavity; *NC*, nerve cord; *Nph*, nephridium; *Npr*, nephropore, *SlGld*, salivary gland; *SlmGld*, slime gland (reservoir); *vm*, ventral muscles.

fibers. Dorsally is a broad, thin band of internal *dorsal longitudinal fibers* (fig. 30, 1), the more median fibers beginning anteriorly at the bases of the antennae, the more lateral ones behind the bases of the oral papillae. Ventrally is a much narrower band of *ventral longitudinal fibers* (2) lying along the midventral line. Between the dorsal and ventral longitudinal muscles is a series of flat, closely adjacent, straplike lateral *dorsoventral muscles* (fig. 29, *dvm*, fig. 30, 3), beginning anteriorly midway between the oral papillae and the first legs. When fully exposed, however, these lateral muscles are seen to be

nearly semicircular in extent (fig. 29), since they are attached dorsally high up on the back external to the dorsal muscles, and ventrally along the midline of the body external to the median ventral muscles.

By removing a section of the lateral muscles and the more lateral fibers of the dorsal muscles (fig. 30, left), there will be exposed two flat *external laterodorsal longitudinal muscles* (4, 5) lying above the leg base, an *external lateroventral longitudinal muscle* (6) mesad of the leg base, two dorsal muscles of the leg (7, 8), and a layer of

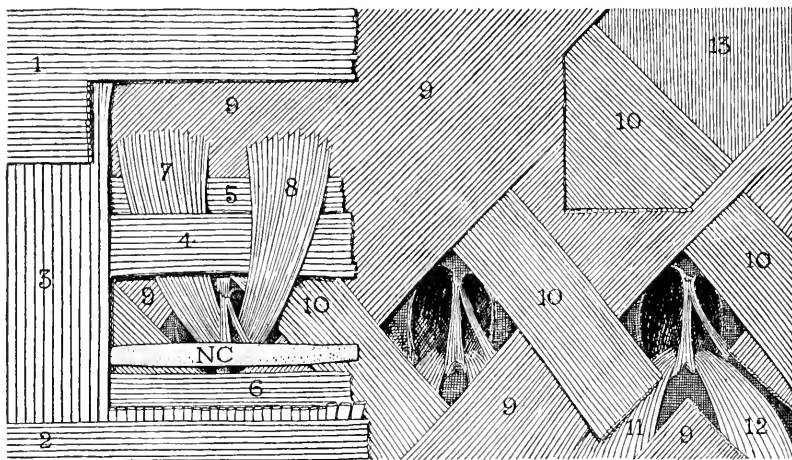


FIG. 30.—Muscles of body wall of *Peripatoides novae-zealandiae* Hutton. The various muscle layers exposed on right side of three successive segmental areas.

1, dorsal longitudinal muscles; 2, ventral longitudinal muscles; 3, dorsoventral lateral muscles; 4, 5, internal and external laterodorsal longitudinal muscles; 6, lateroventral longitudinal muscles; 7, dorsal promotor of leg; 8, dorsal remotor of leg; 9, internal oblique muscles; 10, external oblique muscles (9 and 10, reversed in position between legs); 11, ventral promotor of leg; 12, ventral remotor of leg; 13, circular muscles.

oblique muscles (9, 10). The fibers of the leg muscles penetrate between the oblique fibers to make attachments on the body wall.

The *oblique muscles* (fig. 30, 9, 10) lie external to all the other muscles thus far described. They consist of two thin sheets of fibers crossing each other at right angles in opposite directions. The fibers that are internal on the back (9) go from above downward and forward; those that are external dorsally (10) go downward and posteriorly. Just above each leg, however, a broad band of the external fibers becomes internal by crossing over a similar band of the otherwise internal fibers (9) going below the leg from behind. Between

each two successive legs, therefore, the relation of the two sets of oblique fibers is reversed. On the venter all the fibers again take the same relative position that they have on the back. The two sets of oblique fibers arise on the integument close to the middorsal and midventral lines, and are hence not continuous from one side to the other. External to the oblique fibers may be seen the anterior and posterior ventral muscles of the legs (fig. 30, right, 11, 12).

Finally, outside all the other muscles of the body wall, are the *circular muscles* (fig. 30, 13). They consist of extremely fine fibers closely adherent to the inner surface of the integument, and are apparently continuous across the middorsal and midventral lines.

A few other body muscles occur in the region of the mouth, and the jaws have an elaborate musculature quite different from the musculature of the legs (fig. 21 F).

THE SEGMENTAL APPENDAGES

The appendages of the Onychophora include the antennae, the jaws, the oral papillae, and the legs. Their rudiments appear in the embryo as conical outgrowths of the body wall (fig. 23). The antennae arise from the anterior angles of the cephalic lobes (B, *Ant*) and retain this position. The jaws, which are the appendages of the first postoral somite, arise posterior to the mouth (A, *J*), but later they migrate mesally and forward (B), and are finally buried in the preoral mouth cavity (C), where they become reduced to a pair of double flattened hooks (fig. 21 F) converging in a horizontal plane beneath the mouth (D, *J*). The oral papillae are the appendages of the second postoral somite (fig. 23 A, *OP*), but in the definitive state they take a more anterior position at the sides of the mouth (fig. 21 D, E, *OP*). The legs retain their primary lateroventral positions (fig. 23 B, C), and show but little variation in their final structure.

The onychophoran appendages in their development give no evidence of having been derived from polychaete parapodia; they have no cirri or bristle sacs, and nothing suggests that they are composite organs formed of notopodial and neuropodial elements. The terminal claws of the onychophoran leg in no way resemble parapodial chaetae, and the general structure and musculature of the leg has little in common with a parapodium, except features that adapt each appendage to forward and backward movement on its base. On the other hand, the segmental appendages of the Onychophora and the Arthropoda have the same manner of origin and growth in the embryo, the organs in each case being hollow muscled lobes of the body wall,

and it is only in their later development that they assume the structure characteristic of the adult appendages in each group.

An onychophoran leg (fig. 31 A) is a hollow, conical outgrowth of the body wall terminating in a small pedal lobe bearing a pair of decurved claws. The leg integument is thrown into permanent circular folds, which on the thick basal part of the limb are covered with

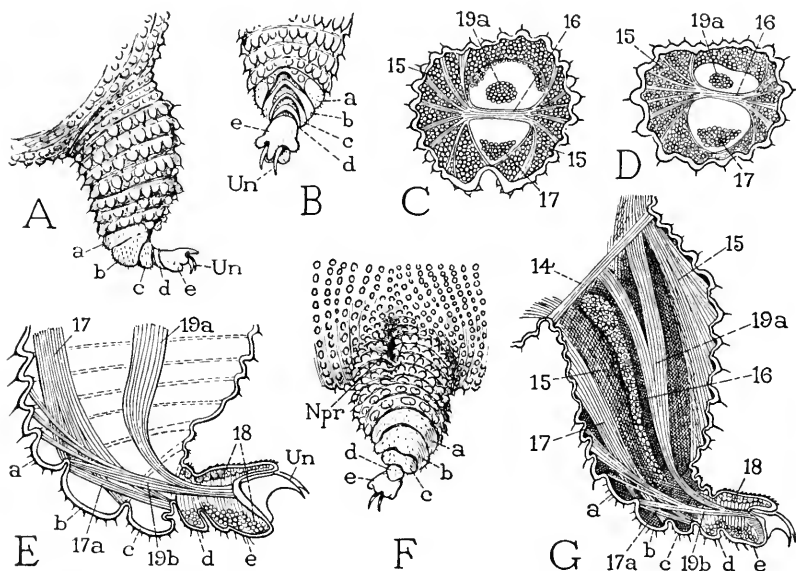


FIG. 31.—Structure and musculature of an onychophoran leg, *Peripatoides novae-zealandiae* Hutton.

A, anterior view of a leg. B, lateral view of distal part of leg. C, horizontal section of basal part of leg. D, section of more distal part of leg. E, diagrammatic vertical section of distal part of leg. F, mesal view of leg. G, section of entire leg in transverse plane of body.

a, b, c, d, distal nontuberculate rings of leg; e, claw-bearing pedal lobe; Npr, nephropore; Un, claws; 14, transverse muscle of leg base; 15, peripheral muscles of basal part of leg; 16, anteroposterior septal muscles of leg; 17, flexor muscle of leg; 17a, flexor of distal leg rings; 18, circular muscles of foot; 19a, 19b, two-branched retractor of claws.

bristle-bearing tubercles. The distal folds, however, form distinct segmentlike rings (A, B, a, b, c, d) and are devoid of tubercles. The pedal lobe (e) appears to be a larger terminal ring bearing the claws (Un).

The leg is movable anteriorly and posteriorly on the obliquely transverse axis of its base by the four somatic muscles (fig. 30, 7, 8, 11, 12) that converge from the body wall into its basal opening. These muscles undoubtedly serve principally as promotors and re-

motors, but are probably also levators and depressors of the leg as a whole. Within the leg the fibers of the four somatic muscles spread out into a thick peripheral layer of intrinsic leg fibers (fig. 31 C, D, G, 15) attached on the successive rings of the thick basal part of the appendage. Running through the narrow axial cavity of the leg is an antero-posterior muscular septum (16), the fibers of which diverge among those of the peripheral layer to the anterior and posterior walls of the leg (C, D). The rest of the leg muscles, except a slender transverse basal muscle (G, 14), are motors of the distal rings and of the claws. The former include a bundle of fibers (17) arising mesally in the leg base (G), with its fibers distributed to the ventral walls of the distal rings (E, G), and a series of strong circular muscles (18) in the pedal lobe. The claws are provided with a large two-branched muscle (E, G, 19), the larger branch arising in the base of the leg (G, 19a), the other in the distal part (E, G, 19b); the short common terminal part is inserted dorsally between the bases of the claws. The claw muscle is, therefore, a levator, or extensor, of the claws and has no antagonist.

It is quite reasonable to suppose that the onychophoran leg is a prototype of the arthropod limb, but if we look for structural resemblances in these two sets of locomotor organs we find few such, if any at all. The differentiation of the onychophoran leg into a thick basal part and a slenderer distal part, and the individualization of the distal rings, on which muscle branches are separately inserted, might be seen as an incipient segmentation. There is, however, no actual parallelism between the structure of the onychophoran leg and that of any arthropod leg, so that all we can say of the former is that it suggests a mode by which segmentation might arise in an ambulatory appendage. We may conclude, therefore, that the appendages of the Onychophora and the appendages of Arthropoda have had a common origin as lobiform outgrowths of the body wall containing extensions of the somatic muscles. The common need of a mechanism for anterior and posterior movement of each appendage on its base then brought about a differentiation of the extrinsic parts of the limb muscles into promotors and remotors, while the parts of the muscles within the leg were elaborated to give greater efficiency to movements of the leg itself. The further course of evolution producing segmentation and correlated musculature in the limb evidently has proceeded independently in the Onychophora and the Arthropoda from a very primitive common beginning, and has gone much farther in the Arthropoda than in the Onychophora.

THE RESPIRATORY ORGANS

The Onychophora are provided with numerous fine tubular ingrowths from the body wall, which undoubtedly serve for respiration, and are therefore termed tracheae, though it is possible that anatomically they are more of the nature of insect tracheoles. The tubules, which are only one to three microns in diameter, arise in dense bundles (fig. 32 B, *Tra*) from small flask-shaped pits (*tp*) of the integument, and extend long distances into the body cavity. The tracheal pits may be very numerous; they occur on all parts of the body, on the head, and around the mouth, but they are most abundant on the back, where several may occupy the space of a square millimeter. For the most part the pits are irregularly distributed, but in some species they are arranged in longitudinal rows. The tracheal bundles issuing from the inner ends of the pits contain large, conspicuous nuclei in their basal parts (*Nu*), which probably pertain to the matrix cells, but the tubes themselves diverge and extend far beyond these nuclei. According to Dakin (1920), the tracheal walls are strengthened by excessively minute but perfect spiral fibers visible in fresh material. In their distal parts the tracheae are branched and go to practically all the internal organs, but their final terminations have not been observed.

Since tracheal invaginations of the body wall are developed for respiratory purposes in nearly all groups of terrestrial arthropods, the mere presence of such organs can have no taxonomic significance, any more than has the presence of gills in diverse groups of aquatic animals. Inasmuch as invertebrates breathe through the skin in any case, evaginations or invaginations of the integument are about the only devices they can develop for improving their respiratory functions.

THE CIRCULATORY SYSTEM

The blood vascular system of the Onychophora consists only of a tubular dorsal vessel (fig. 29, *DV*) extending the entire length of the body, said to be open anteriorly and posteriorly. The walls of the vessel consist of circular muscle fibers, and are perforated dorsally in each segment by a pair of ostia. The tube is suspended from the body wall by connective tissue strands, and is supported on a membranous and muscular dorsal diaphragm (*DDph*). The diaphragm muscles are fine, regularly transverse fibers medially attached on the ventral wall of the blood vessel; laterally they penetrate between the fibers of the dorsal somatic muscles and are apparently attached on

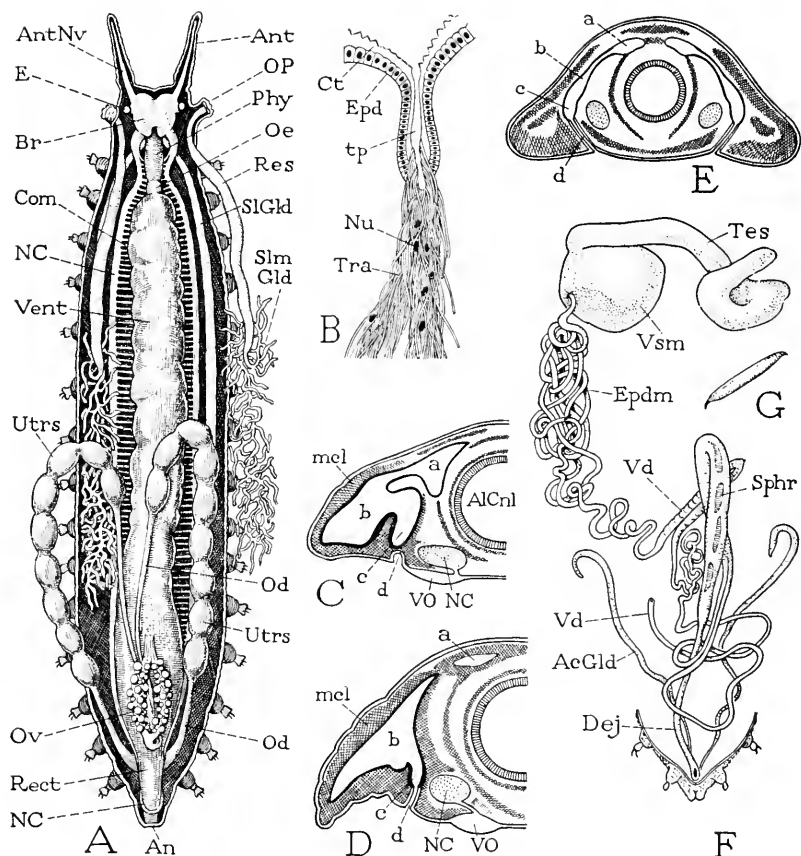


FIG. 32.—Internal structure of Onychophora, and later development of the coelomic sacs.

A, general view of internal anatomy of *Peripatoides novae-zealandiae* Hutton, female, dorsal view; muscles, nephridia, peripheral nerves, and dorsal blood vessel omitted. B, tracheal pit of *Peripatopsis capensis* Grube and respiratory tubules extending inward from it (from Schneider, 1902). C, section of embryo of *Peripatus edwardsi* Blanchard, showing constriction of coelomic cavity into dorsal gonadal compartment (a) and lateral nephridial compartment (b); rudiments of coelomoduct (c, d) not yet united (from Kennel, 1888). D, same, later stage, dorsal compartment (a) of coelomic sac (which later disappears except in genital somites) and nephridial compartment (b) entirely separated, coelomoduct (c, d) open to exterior (from Kennel, 1888). E, section of embryonic somite of genital outlets, coelomic sacs narrowed but not divided as in other segments (C, D), continuous from gonads (a) through coelomoducts (d) to exterior (from Kennel, 1888). F, male reproductive organs of *Peripatopsis blainvilliei* Gay-Gervais (from Bouvier, 1902, with accessories omitted). G, spermatophore of same (from Bouvier, 1902).

a, dorsal gonadal compartment of coelomic sac; AcGld, genital accessory gland; AlCnl, alimentary canal; Ant, antenna; AntNv, antennal nerve; b, nephridial compartment of coelomic sac; Br, brain; c, mesodermal component of coelomoduct; Com, nerve commissures; Ct, cuticula; d, ectodermal component of coelomoduct; Dej, ductus ejaculatorius; E, eye; Epd, epidermis; Epdm, epididymis; mcl, muscle; NC, nerve cord; Nu, nucleus; Od, oviduct; Oe, oesophagus; OP, oral papilla; Ov, ovary; Phy, pharynx; Res, reservoir of slime gland; Rect, rectum; SlGld, salivary gland; SlmGld, slime gland; Sphr, spermatophore; Tes, testis; tp, tracheal pit; Tra, tracheal tubules; Utrs, uteri; Vd, vas deferens; Vent, ventriculus; VO, ventral "organ"; Vsm, vesicula seminalis.

the body wall. Above the diaphragm on each side of the blood vessel are masses of small individual cells, probably "nephrocytes." The circulatory system of the Onychophora thus resembles that of the Chilopoda and the Hexapoda in the simplicity of its structure. Since many of the arthropods, in common with the annelids, have a highly developed blood vascular system, it would seem probable that the simpler forms represent reductions from a more elaborate primitive system such as that of the Annelida.

THE NEPHRIDIA

The nephridiallike excretory organs of the Onychophora are paired segmental structures usually present in all the somites between the somite of the oral papillae and that of the genital ducts, though they may differ much in size and in the relative development of their parts. They lie in the lateral compartments of the definitive body cavity at the bases of the legs (fig. 29, *Nph*), and open externally in grooves on the ventral surfaces of the leg bases (figs. 29, 31 F, 33 A, *Npr*), except those of the fourth and fifth pairs, which in most species open at the bases of the distal rings of the legs (fig. 33 C).

A well-developed onychophoran nephridium consists of five distinct parts (fig. 33 A): First, beginning externally, is a short outlet duct (*Nd*); second, a bladderlike enlargement, or reservoir (*Bl*); third, a tubular canal (*Cnl*) varying in length and usually coiled; fourth, a funnel-shaped enlargement of the inner end of the canal (*Fun*); and fifth, a thin-walled end-sac (*ESc*). The walls of the funnel (*B*) are relatively thick and are histologically different from the rest of the canal; they are clothed with long vibratile cilia directed toward the nephridial exit (see Dakin, 1920, Cuénot, 1926, Zilch, 1936).

The funnel and the canal of an adult onychophoran nephridium are comparable with an entire metanephridium of the annelids; the end-sac is a remnant of the coelomic sac of the embryonic somite. The opening of the nephridial funnel into the end-sac, therefore, is the nephrostome (fig. 33 B, *Nst*). The canal is developed in the embryo as an exit duct of the coelomic sac, formed by the union of a ventral diverticulum of the sac (fig. 32 C, *c*) with a tubular ingrowth (*d*) from the ectoderm of the same segment mesad of the leg rudiment (*D*). The primitive function of the coelomoducts undoubtedly was the discharge of excretory products and, in the genital segments, of the gametes. Embryonic coelomoducts occur, according to Evans (1902), in connection with the coelomic sacs of the antennae (fig. 27 D, *d*), and in all the postoral somites except

the somite of the jaws. During embryonic development the coelomic sacs of those segments that eventually contain nephridia become each constricted into a dorsal section (fig. 32 C, *a*) and a ventral section (*b*), which soon become entirely separate compartments (D). Except in the genital region the dorsal compartments disappear; in the nephridial somites the ventral compartments become much reduced, but they retain their open connections with the coelomoducts, and persist as the delicate end-sacs of the nephridia (fig. 33, *ESc*).

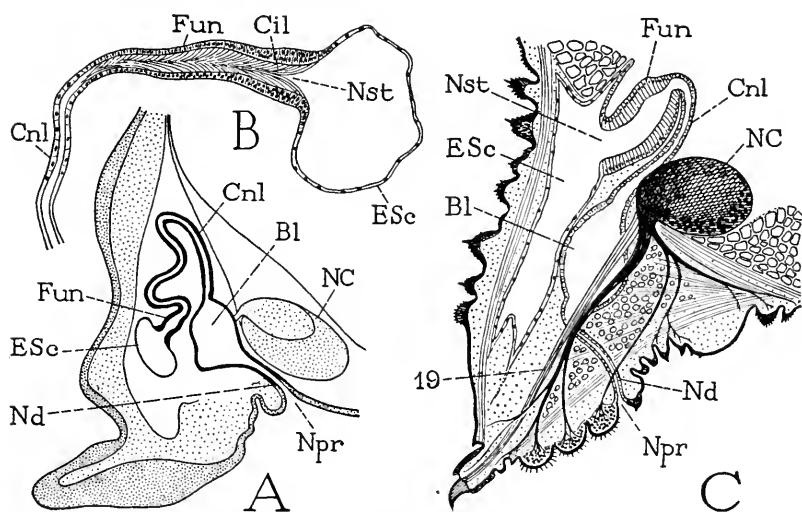


FIG. 33.—Structure of onychophoran nephridia.

A, diagrammatic transverse section of leg and nephridium of mature embryo of *Peripatopsis capensis* Grube (from Sedgwick, 1888). B, inner part of nephridium of *Peripatoides* sp., showing ciliated funnel (*Fun*) with nephrostome opening into coelomic end-sac (from Dakin, 1920). C, diagrammatic transverse section of leg and nephridium of adult *Peripatus tholloni* Bouvier (from Fedorow, 1926).

Bl, nephridial bladder; *Cil*, cilia; *Cnl*, nephridial canal; *ESc*, coelomic end-sac of nephridium; *Fun*, nephridial funnel; *NC*, nerve cord; *Nd*, nephridial duct; *Npr*, nephropore; *Nst*, nephrostome.

It is commonly held that the excretory organs of the Onychophora are homologous with the annelid metanephridia (see Glen, 1919). The simple development of the canals as open ventral diverticula of the coelomic walls (not of the septa), the direct opening of the canals to the exterior on the same segment, and the occurrence of embryonic coelomic ducts in the head, however, are all features distinctive of the Onychophora. Considering, therefore, that there is little probability on other grounds that the Onychophora have been derived from annelids having metanephridia, we may conclude that the open

nephridia of the higher Annelida and the coelomic exits of the Onychophora have been separately acquired and developed in each group. On the other hand, there can be little doubt that the nephridial organs of Arthropoda (antennal, maxillary, and coxal glands) are entirely comparable with the onychophoran nephridia.

THE ORGANS OF REPRODUCTION

In the evolution of specific reproductive organs the Onychophora are far in advance of any of the polychaete or oligochaete annelids; but the development and the definitive structure of the genital organs are so closely parallel in the Onychophora and the Arthropoda that we can scarcely question the probability of the genital systems in these two groups having had a common origin. In fact, it is the fundamental similarity in the genital system that would appear to constitute the closest bond of union between the Onychophora and the Arthropoda, and which most strongly suggests that the two groups have been derived from a common progenitor. The germinal centers of the Onychophora, as in the arthropods, are entirely enclosed in gonadial sacs of coelomic derivation, and the gametes are discharged through ducts whose lumina are continuous with those of the gonads. An approach to a closed genital system is seen in the Oligochaeta in the development of coelomic seminal vesicles containing the genital outlet funnels, and a system as completely closed as that of the Onychophora and Arthropoda is perfected in the Hirudinea; but the ontogeny of the organs in these several groups shows that there is no possibility of the onychophoran-arthropod reproductive system having been evolved from that of the higher annelids.

The primary germ cells of the Onychophora become localized at an early stage of embryonic development in the median dorsal parts of the splanchnic walls of one or several posterior pairs of coelomic sacs (fig. 34 A, *Grm*). According to Evans (1902) there are four embryonic genital somites in *Eoperipatus weldoni*, while Kennel (1888) says the germ cells of *Peripatus edwardsi* occur in but one somite. Whatever the number of genital segments may be in modern forms, we must suppose that the germ cells once occupied most of the somites, for the early embryonic relation of the germinal centers to the coelomic sacs is identical with the adult condition in the Polychaeta, and undoubtedly means that in the primitive Onychophora the gametes were discharged into the coelomic sacs (A, *Spz*), and were liberated from the latter through the coelomoducts (*d*). As we have seen, the upper parts of all the coelomic sacs between

the somite of the oral papillae and the somite of the genital ducts become constricted from the ventral parts (fig. 32 C, *a*), and then separated as independent dorsal compartments (D, *a*). In the pre-genital somites the dorsal compartments disappear, but in the definitive genital somites they persist as gonadial sacs containing the germaria (fig. 34 C, *G*). The gonadial sacs of each lateral series,

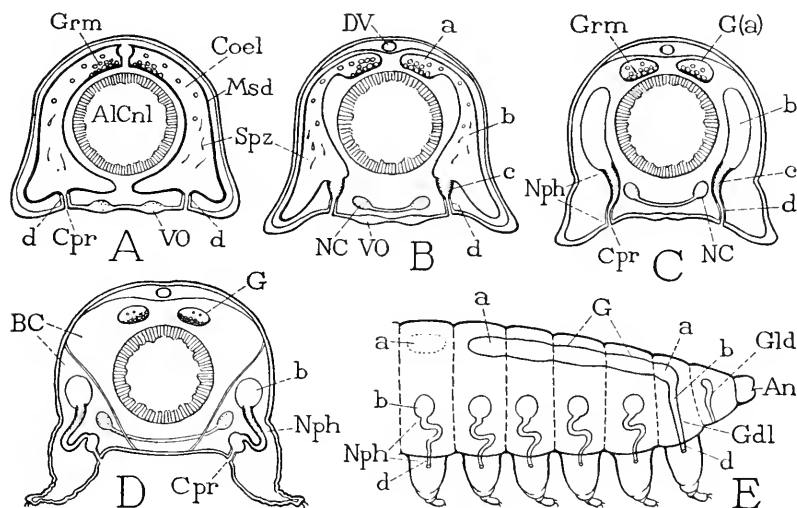


FIG. 34.—Diagrams showing the transformation of the onychophoran coelomic sacs and coelomoducts into genital organs and nephridia. (From Snodgrass, 1936, based on Sedgwick, 1885, Kennel, 1888, and Evans, 1902.)

A, theoretical primitive stage in which excretory products and the gametes were discharged from the coelomic sacs through coelomoducts. B, C, D, differentiation and division of the coelomic sacs into dorsal gonadial sacs (*a*) and ventral nephridic sacs (*b*), the last finally reduced (D) to end-sacs of the nephridia. E, gonadial sacs of definitive genital segments united on each side in a gonadial tube (*G*) opening through undivided coelomic sac of penultimate somite.

a, gonadial compartment of primitive coelomic sac; *AlCnl*, alimentary canal; *An*, anus; *b*, nephridic compartment of coelomic sac; *BC*, definitive body cavity (haemocoel); *c*, nephridial diverticulum of coelomic sac; *Coel*, coelomic cavity; *Cpr*, coelomopore; *d*, ectodermal part of coelomoduct; *DV*, dorsal blood vessel; *G*, gonad; *Gdl*, lateral gonoduct; *Gld*, accessory genital gland; *Grm*, germarium; *Msd*, mesoderm; *NC*, nerve cord; *Nph*, nephridium; *Spz*, spermatozoa; *VO*, ventral "organ" of ectoderm.

however, unite in a continuous tube (E, *G*), which becomes the definitive gonad with a germinal band in its ventral wall (C, D, *G*). Furthermore, the posterior ends of the gonadial tubes open into the coelomic sacs of the following somite, and these sacs, which maintain their integrity, and their continuity with the coelomoducts (fig. 32 E, *a*, *b*, *c*, *d*), become the lateral genital ducts (fig. 34 E, *Gdl*). Eventu-

ally the apertures of the lateral ducts come together on the midline of the venter, where they are carried inward at the end of an ectodermal invagination that forms a common definitive exit tube, the ejaculatory duct or median oviduct.

The adult reproductive organs of the Onychophora are strikingly arthropodan in character. In the male, the testes retain the tubular embryonic form (fig. 32 F, *Tes*); each discharges into a seminal vesicle (*Vsm*) from which proceeds a long tubular vas deferens (*Vd*), the anterior part of which is thrown into an epididymislike mass of coils (*Epdm*). The ejaculatory duct (*Dej*) is usually long and irregularly looped; its opening is on the region of the penultimate somite. Associated with the gonopore is a pair of tubular accessory glands (*AcGld*), said to be the reduced coelomic sacs of the last somite (fig. 34 E, *Gld*). In the female, the tubular ovaries are united at their extremities and lie on the dorsal surface of the alimentary canal in the posterior part of the body (fig. 32 A, *Ov*). The oviducts (*Od*) proceed first forward from the posterior ends of the ovaries, and then turn backward to unite beneath the rectum (*Rect*) in a very short terminal atrium, or common oviduct, opening in the same position as the gonopore of the male. In viviparous species the intermediate parts of the oviducts are enlarged in a series of uterine chambers (*Utrs*) containing the embryos. Sperm receptacles usually occur on the lateral oviducts near their ovarian ends.

VI. THE ARTHROPODA

The fundamental characters of the arthropods are those of the Onychophora and the Annelida. The three groups have in common the following features: (1) The ventral elongation of the blastopore and the closure of its intermediate part, resulting in the formation of a tubular enteron with a ventral subapical mouth and a terminal anus, and in the conversion of the preblastoporic region of the trunk into a prostomial cephalic lobe; (2) a definitive tripartite alimentary canal composed of the primitive endodermal enteron, and of a secondary ectodermal stomodaeum and proctodaeum; (3) the differentiation of a part of the mesoblast, originally formed in the posterior end of the body, into a specific mesoderm taking the form of ventrolateral bands that extend forward through the entire length of the body and penetrate into the prostomium; (4) metamerism of the somatic ectoderm and mesoderm, involving a segmental repetition of organs derived from these germ layers; (5) the continuity of the acronal centers of the primary nervous system with the somatic centers

secondarily developed in connection with metamerism; (6) internal cleavage of the mesoderm segments to form paired coelomic cavities; (7) a somatic muscular system applied against the body wall, consisting primarily of an outer set of constrictor fibers running in transverse planes, and of an inner set of contractor fibers taking a longitudinal course, each of which may be variously amplified or reduced; (8) the development of a blood vascular system from the mesoderm, composed essentially of a dorsal and a ventral longitudinal vessel connected by lateral vessels, but often reduced to a dorsal vessel and more or less well-defined sinuses; (9) the association of the germ cells with the walls of the coelomic sacs, and their discharge into the coelom.

The common basic features of organization above enumerated attest the origin of the Arthropoda, the Onychophora, and the higher Annelida from a common ancestral form, which itself must necessarily be visualized as a generalized annelid. It is to be assumed that the progenitors of the three groups had already acquired a lengthened body by the addition of secondary genital somites proliferated from a subterminal zone of growth. Though teloblastic growth does not appear in the ontogeny of the Onychophora, it is quite as characteristic of certain arthropods as of the annelids.

The Arthropoda have in common with the Onychophora the following nonannelid characters: (1) A chitinous ectodermal cuticula; (2) segmental ambulatory appendages formed as simple outgrowths of the body wall, which in their structure and development give no suggestion of a community of origin with the composite parapodia of the Polychaeta; (3) segmental excretory organs (antennal, maxillary, and coxal glands) that resemble the nephridia of Onychophora in being remnants of coelomic sacs connected with the exterior by simple coelomoducts, but which have neither the anatomical position nor the development of annelid metanephridia; and (4) closed gonadal sacs of coelomic origin, containing the germarial centers in their walls, and connected with the exterior by a pair of coelomic sacs set apart to serve as genital ducts. A feature characteristic of both the Arthropoda and the Onychophora is the restoration of the haemocoel as the definitive body cavity, resulting from the reduction of the coelom to the cavities of gonadal and nephridial sacs, but it is not distinctive of them because an obliteration of the coelom occurs also in certain annelids.

The small but important assemblage of characters given above as common to the Onychophora and the Arthropoda would seem to indicate that the two groups have been evolved from the same ancestral

stock, which arose from some generalized nonchaetopodous annelid; but since none of the modern annelids has these characters it is evident that the annelidan progenitors of the Protonychophora-arthropoda have left no direct descendents. The Arthropoda differ in so many respects from present-day Onychophora that it is certain they must have branched off from the common onychophoran-arthropod trunk before the latter had gone far in the onychophoran direction. Arthropod forms were highly developed and differentiated in the early Cambrian period of geological history, and must, therefore, have had their origin in remote pre-Cambrian times, though in the rocks of this period there is no specific evidence of their existence.

As an individualized group, the Arthropoda are characterized particularly by the development of hard plates in the cuticular layer of the integument, separated by areas of flexibility. In the Mandibulata sclerotization results from the presence of nonchitinous substances in the otherwise chitinous cuticula; in the Trilobita and Chelicerata sclerotization may be due to a structural differentiation of the chitin itself, though apparently little attention has been given to the chemical composition of the cuticular skeleton in these groups. Ruser (1933) describes the physical structure of "hard chitin" and "elastic chitin" in the Ixodidae, but makes no determination of their chemical nature.

Since the muscles are primarily attached on the body wall, the differentiation of the latter into hard and flexible areas at once created a possibility for unlimited development of skeleto-muscular mechanisms, and it is through the elaboration of such mechanisms that the arthropods have attained their exalted position among the articulates, and their wonderful diversity of structure. It is true, of course, that some of them, particularly those that have taken up parasitic habits, have renounced their birthright, and among the latter we find examples of physical degeneration carried to such an extent that every semblance of arthropod structure may be lost.

Sclerotization of the integument involved first a complete change in the mechanism of body movement, for if the rings of flexibility between segmental plates remained at the primary intersegmental grooves, on which the longitudinal muscles are attached, there would be little if any possibility of movement. Hence, each dorsal and ventral plate includes the primary intersegmental groove in front, while the areas of flexibility occupy the posterior parts of the segmental regions. The sclerotized parts of the primary intersegmental grooves, carrying the muscle attachments, thus come to form internal ridges, or antecostae, on or near the anterior margins of the definitive

tergal and sternal plates, and the primary intersegmental grooves become the submarginal antecostal sutures. As a consequence, a new, *secondary* type of segmentation has been established, in which the functional intersegmental rings are the membranous posterior parts of the primary segments, and the action of the longitudinal muscles becomes intersegmental instead of intrasegmental. A body mechanism of this kind is typical of all the arthropods, but still it is by no means fixed, for innumerable modifications of it have been introduced in adaptation to the development of special structures for specific purposes.

The acquisition of an exoskeleton necessarily limits freedom of body movement, such as that possessed by the highly flexible annelids, but at the same time it furnishes a mechanism by which movements may become more specific, since the development of definite hinge joints becomes possible, and muscles can assume more effective antagonistic relations to each other. The longitudinal muscles lose nothing of their efficiency, but their contraction now results in a telescoping of the body segments. The presence of dorsal and ventral plates, however, necessarily eliminates the constrictor effect of the primitive circular or semicircular muscles; the latter, therefore, have become reduced to lateral tergosternal muscles, the contraction of which produces a flattening of the body. The primitive mechanism of dilation and extension by unequal distribution of internal pressure is still operative; but the potentiality of developing endoskeletal structures gives the possibility of a new mechanism of expansion, for the ingrowth of apodemal arms from tergal or sternal areas, on which primarily compressor muscles are attached, may reverse the position of such muscles to the extent that they become dilators. A separation of contiguous plates, however, may be brought about also by the contraction of intersegmental muscles that have been reversed by the overlapping of the plates. All these mechanical devices and many others are variously and often highly developed in the different arthropod groups, and their elaboration has set the arthropods far above the annelids and onychophorons in the power of performing definite and specific acts. Even the wing mechanism of pterygote insects has been built up from little more than the skeletal parts and musculature common to the body segments. It should be observed, however, that although the musculature of the body segments and the appendages is fairly definite and fixed within the major arthropod groups, there seems to be no limit to the potential genesis of new muscles in connection with special organs, such as the male genitalia of insects, and, furthermore, that the entire body musculature is

subject to adaptive changes, which may be very extensive, as in certain holometabolous insect larvae.

Sclerotization of the integument has affected not only the wall of the body, but also the walls of the tubular segmental appendages, and the latter are jointed by definite rings of flexible membrane interposed between the resulting limb segments, or podomeres. Hence, the arthropod limb itself has possibilities of much variety and specificity of action. As a consequence, while probably the appendages in the first place were all simple locomotor organs, many of them have been converted into instruments adapted to various purposes, and those that still subserve the locomotor function are capable of all the kinds of mechanical progression except flying known among animals.

Concomitant with the evolution of the skeleto-muscular mechanisms, the nervous system and the sense organs have necessarily acquired a high state of development, and the elaboration of most intricate instincts has been possible because of the facility with which tools may be produced and adapted to their ends.

The primitive arthropods, being closely related to the primitive onychophorons, and together with the latter derived from generalized annelids, must have been slender, many-segmented, polypodous creatures resembling modern centipedes. They differed from their contemporaneous onychophoran relatives in having dorsal and ventral segmental plates and specifically jointed appendages. The Protarthropoda were early differentiated into primitive trilobites and primitive mandibulate forms. From the primitive trilobites were evolved the later Trilobita, Xiphosurida, Eurypterida, and Arachnida, while the Protomandibulata gave rise to the Crustacea, the Diplopoda, the Chilopoda, and the Hexapoda.

EARLY EMBRYONIC DEVELOPMENT

The processes of cleavage and germ-layer formation are so variable among the arthropods that they can have little value in a phylogenetic study of arthropod relationships. Cleavage, whether total or partial, results usually in the formation of a superficial blastoderm, and the embryo appears as a germ band on the ventral side of the egg. Gastrulation in some of the Crustacea takes place by invagination, but more commonly both the endoderm and the mesoderm are formed by delamination or by proliferation from the blastoderm or the germ band. Manton (1928) gives a precise account of the proliferation of the germ layers and the primary germ cells from the blastoporic region in the crustacean *Hemimysis*, the cells of the several groups

being first differentiated on the surface of the germinal disk. The first endoderm cells in many of the arthropods scatter through the yolk as independent trophocytes (vitellogophs) and the definitive enteron may then be formed either by a reassembling of the cells about the yolk, or by regeneration from intact endodermal rudiments.

The mesoderm in some of the Crustacea, Chilopoda, and Chelicerata is proliferated forward from a posterior generative zone very much in the manner of the onychophoran mesoderm, and suggestive of the teloblastic origin of the coeloblast in the Annelida. Among the Crustacea there are in fact a few cases in which the mesoderm takes its origin, at least in part, from a single pair of teloblastomeres derived from the endoderm, as in the cirriped *Lepas*. The mesodermal telo-

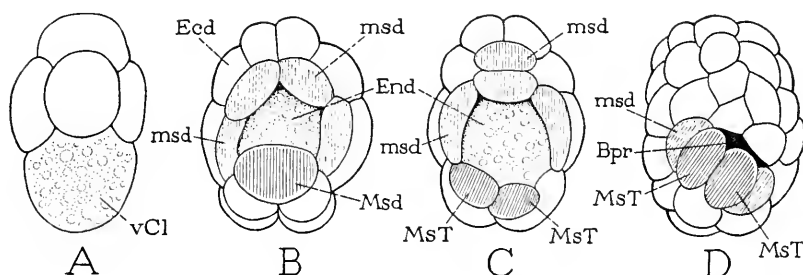


FIG. 35.—Early stages in the development of a cirriped, *Lepas*. (Simplified from Bigelow, 1902.)

A, 8-cell stage, with large yolk-filled posterior cell. B, 30-cell stage, endoderm surrounded by mesoderm comprising a posterior cell (*Msd*) of endodermal origin, and four cells (*msd*) of ectodermal origin. C, the posterior mesoblast cell divided into mesodermal teloblasts (*MsT*). D, near close of gastrulation, but with mesoderm cells still exposed.

Bpr, blastopore; *Ecd*, ectoderm; *End*, endoderm; *Msd*, endodermal mesoderm; *msd*, ectodermal mesoderm; *MsT*, mesodermal teloblast; *vCl*, yolk-filled cell at vegetative pole of morula.

blasts of *Lepas*, according to Bigelow (1902), appear in the 32-cell stage on the posterior lip of the blastopore (fig. 35 C, *Mst*), and are produced from a single mesoblast cell (B, *Msd*) that results from the division of a primary yolk-filled blastomere (A, *vCl*) at the posterior pole of the morula. Four other mesoblast cells, however, are formed in *Lepas* from the ectodermal lips of the blastopore (B, C, *msd*), and eventually the entire mesoblast sinks into the blastopore (D). A separate destiny of the mesoblast from the two sources, entoblastic and ectoblastic, has not been distinguished in *Lepas*, but it is a point of much interest to note that here the mesoblast *completely surrounds the open blastopore* between the ectoderm and the endoderm, a part of it being of endodermal and a part of it of ectodermal

derivation. It is not difficult, then, to understand from this condition how, in forms having a *closed* blastopore, the coelomic mesoblast may arise from the entire length of the linear blastoporic area, and we may further see some significance in the statement by Sedgwick (1887) that in the onychophoron *Peripatopsis* the mesoderm bands in their forward growth are augmented by cells derived from the lips of the blastopore. In the more specialized types of arthropod development evidence of teloblastic generation of the mesoderm is entirely lost, or at least obscured, and the whole of the mesoderm appears to be a direct product of the germ band closely associated with the endoderm. In its full development the arthropod mesoderm surrounds the blastopore anteriorly, since in the adult the lateral bands of the cephalic mesoderm may be continuous from side to side in front of the mouth.

Segmentation of the mesoderm and the subsequent formation of coelomic sacs take place in the early embryonic stages of many Crustacea and Arachnida almost as completely as in the Onychophora and Annelida, but in the myriapods the coelomic sacs are small, and in the insects they are for the most part represented only by cleavage spaces in the lateral parts of the mesoderm. In all cases, however, the walls of the sacs break down, except such parts of them as are retained in the formation of certain organs of coelomic origin, and the haemocoel is restored as the definitive body cavity. Probably all muscle tissue of the arthropods is produced from the coelomic mesoblast; though some writers have claimed that certain muscles are produced directly from the ectoderm, the evidence is open to question and needs closer scrutiny (see Needham, 1937).

PRIMARY AND SECONDARY SOMITES

There is ample reason from arthropod ontogeny for believing that the arthropods have been derived, as have the annelids, from primitively unsegmented ancestral forms in which metamerism first appeared as a direct subdivision of the primary body region into a small number of somites, and that the subsequent increase in the number of somites proceeded secondarily from growth in a subterminal zone of undifferentiated cells. This dual method of somite production is recapitulated in the embryogeny of some of the arthropods, and teloblastic growth is of frequent occurrence in postembryonic development.

In the Trilobita it seems very probable, as contended by Iwanoff (1933) and Schulze (1936), that the so-called head represents the

area of primary segmentation, for there is no doubt that the post-cephalic segments are produced by teloblastic growth. The youngest trilobite larvae known give no evidence of metamerism (fig. 46 A), but there soon appears in the glabellar region four pairs of lateral impressions or transverse grooves that divide the glabella into five consecutive lobes (fig. 36 A). These depressions produce internal

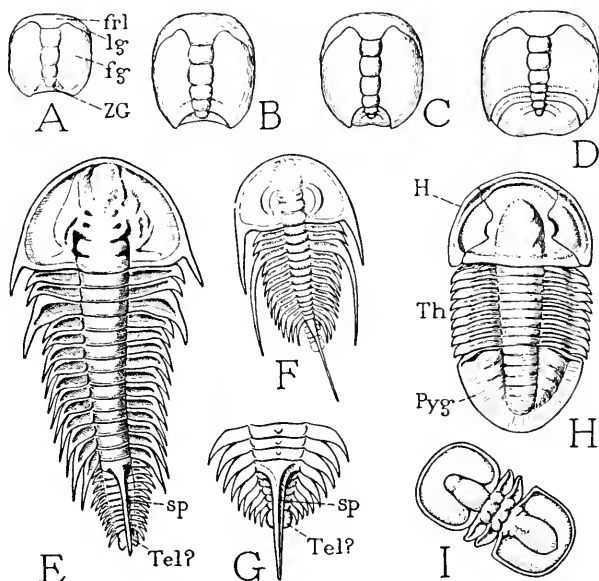


FIG. 36.—Segmentation and tagmosis of Trilobita.

A-D, four successive stages in larval development of *Liostracus linnarssoni* Brögger (from Warburg, 1925). E, *Olenellus vermontanus* Hall (from Walcott, 1910). F, *Olenellus gilberti* Meek (from Walcott, 1910). G, *Schmidtiellus mickwitzii* Schmidt, distal body segments (from Walcott, 1910). H, *Asaphiscus wheeleri* Meek, example of a trilobite with distal segments united in a caudal fan, or pygidium (from Walcott, 1916). I, *Agnostis montis* Matthew, example of the group Agnostia having only two free segments between head and pygidium (from Walcott, 1908).

fg, fixed cheek, or fixigene; *frl*, frontal lobe; *H*, head; *lg*, free cheek, or librigenae; *Pyg*, pygidium; *sp*, spine; *Tel*, terminal lobe of body, probably the telson; *Th*, thorax; *ZG*, zone of growth.

ridges or apodemes most probably for muscle attachments, and their formation, therefore, does not represent the process of segmentation itself, but unquestionably they mark the primary intersegmental lines of the segments united in the larval body. The first glabellar division, known as the frontal lobe (A, *frl*), is continuous with a pair of lateral areas (*lg*) that become the "free cheeks" of the adult bearing the compound eyes (fig. 46 E, *lg*). The frontal lobe, therefore, may

be regarded as a part of the eye segment, or acron, and further reasons for so regarding it will be given later. The other four glabellar lobes must then represent four primary larval somites, the intersegmental lines of which should, theoretically, have extended to the lateral margins of the simple oval body before segmentation in the latter was suppressed. The postlarval somites of the adult trilobite are generated teloblastically (fig. 36 B, C, D) from a small region of the larva behind the glabella (A, *ZG*), and are, therefore, clearly secondary somites. The definitive segments of the postcephalic series remain distinct in some of the trilobites to the end of the body (E, F), where there is a small terminal lobe (E, G, *Tel?*) that may be the telson; in others the posterior segments are united in a tail-fan, or pygidium (H, *Pyg*), and in the *Agnostia* (I) only two segments retain their independence between the head and the pygidium.

The Xiphosurida in the adult stage resemble the Trilobita in so many respects that we should expect to find an even closer approach to the trilobite structure in their developmental stages; and, in fact, it has been shown by Iwanoff (1933) that the primary segmentation in the embryo of *Limulus moluccanus* produces four somites (fig. 37 A, *I-IV*), those of the chelicerae, the pedipalps, and the first two pairs of legs, which evidently represent the four postacronal head somites of a trilobite. Because of the large amount of yolk in the ectoderm, embryonic metamerism appears first in the mesoderm, which is early divided almost simultaneously into four sections corresponding with the four primary somites. The preoral cephalic region of *L. moluccanus*, Iwanoff says, is at first not distinctly differentiated from the surrounding blastoderm, but later it becomes apparent as a preoral head segment without appendages, and in an older embryo it forms a pair of definite cephalic lobes (B, *Prc*). Behind the fourth somite there is in the young embryo (A) only an unsegmented tail piece, but at the base of this region are later generated consecutively (B) the remaining segments of the adult, which are thus typically teloblastic in the manner of their formation.

It would thus appear that the primary segmentation of the ancestors both of the trilobites and the xiphosurids produced only four somites. These four primary somites, united with one another and with the cephalic lobe, or acron, constitute the "head" in the Trilobita (fig. 36 H, *H*); in the Xiphosurida they form the anterior part of the prosoma, for in this group three following somites and part of a fourth are combined with the four primitive somites in the anterior section of the body (fig. 47 E). Moreover, in the Xiphosurida a union has taken place between all the opisthosomatic somites, so that

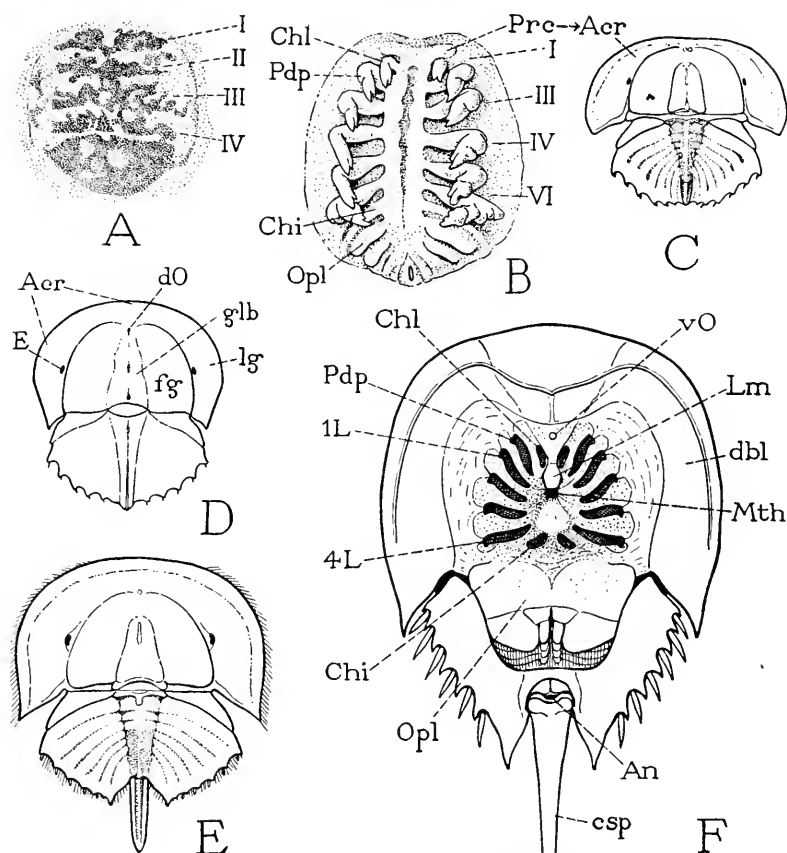


FIG. 37.—Embryonic and adult segmentation of *Limulus*. (A-E from Iwanoff, 1933.)

A, *Limulus moluccanus* Linn., germ band with mesoderm divided into four postoral somites, cephalic lobes not yet differentiated from blastoderm. B, same, embryo with nine pairs of appendages, cephalic lobes (*Prc*) present. C, first instar larva, segments of opisthosoma indicated by internal mesoderm bands before moulting. D, first instar larva before moulting stage. E, second instar larva. F, *Limulus polyphemus* Linn., young adult, ventral view, prosomatic appendages removed, showing radial position of their bases around the central mouth.

Acr, acron, derived from procephalic lobes of embryo; *An*, anus; *Chi*, chilarium; *Chl*, chelicera; *csp*, caudal spine; *dbl*, doublure; *dO*, dorsal ocellus; *E*, compound eye; *fg*, fixigene; *glb*, glabella; *I-VI*, first six somites; *L*, leg; *lg*, libragene; *Lm*, labrum; *Mth*, mouth; *Opl*, genital operculum; *Pdp*, pedipalp; *Prc*, procephalic lobe; *vO*, ventral ocellus.

there is no intermediate region of free somites as in the Trilobita and Agnostia (fig. 36 H, I).

The adult structure of *Limulus* contains evidence of the presence of 14 postoral somites, the last somite being behind the last gill-bearing segment (fig. 47 D, XIV); but Iwanoff (1933) says that in the embryo rudiments of three somites appear in the postbranchial region, giving thus a total of 16 somites anterior to the caudal spine. The caudal spine of the Xiphosurida is often called the "telson," but, as shown by Schulze (1936), a comparison with the subterminal spine of such trilobites as *Mesonacis* and *Olenellus* (fig. 36 E, F, G), which arises from a segment some distance from the end of the body, suggests that the caudal spine of the xiphosurids may not be a true terminal structure, and that several primitive somites beyond it may have been lost.

Studies on the embryogeny of Arachnida have not brought out any distinction between primary and secondary somites, and the arachnids have no postembryonic teloblastic growth. Schulze (1936), however, has pointed out many features in the adult structure of the arachnids, especially in the Acarina, that suggest the trilobite type of segmentation. The area of the four primary somites, he shows, is often evident as a differentiated anterior region of the prosoma, and in the segmentation and body form of such acarids as *Oxypleurites* there may be seen a striking general resemblance to a mesonacid trilobite. The arachnid prosoma contains six postacronal somites, and in this respect, therefore, is intermediate between the trilobite "head" and the xiphosurid prosoma.

The embryonic development of segmentation in the Crustacea has been particularly studied by Sollaud (1923) in the palaemonid *Leander*. The germ band of *Leander* is at first V-shaped (fig. 38 A), its two arms diverging forward on the blastoderm from a posterior area of proliferation (GD) in the region of the blastopore, whence also are proliferated forward two corresponding bands of mesoderm. Each mesoderm band soon becomes divided into four consecutive parts, which appear as four lobes on the surface (B). The germ bands themselves gradually become less divergent, and finally their anterior ends curve mesally and unite by a bridge between their anterior lobes (C). At the same time the rudiments of three pairs of appendages appear on the second, third, and fourth lobes, which are respectively the first antennae (B, D, 1Ant), the second antennae (2Ant), and the mandibles (Md). The first lobes (Prc) have no appendages, but they give rise to the compound eyes and the optic ganglia. There now appear in the ectoderm of the young embryo,

Sollaud says, three transverse grooves which define the first segmentation (D). The most anterior groove runs between the first and second pairs of antennae, the next between the second antennae and the mandibles, and the third behind the mandibles. The body of the embryo is thus divided into an anterior prostomial head segment

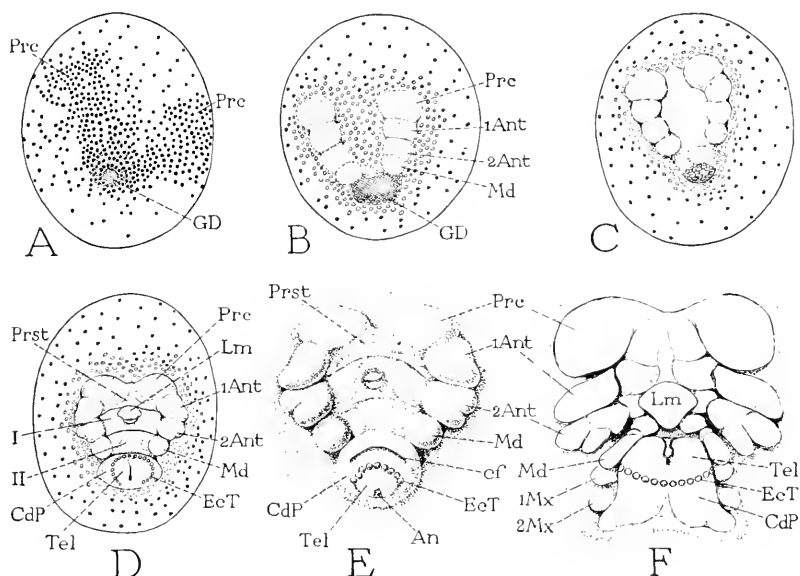


FIG. 38.—Early embryonic stages of a palaemonid crustacean, showing the development of the procephalic lobes and the antennules from the unsegmented prostomial region, and the formation of four primary body somites. (From Sollaud, 1923.) A, *Leander squilla* Linn. B-F, *L. serratus* Pennant.

A, ventral surface of egg showing germinal disk and anterior proliferation of germ bands. B, early nauplius stage with first appearance of appendages. C, later stage with germ bands united anteriorly. D, nauplius stage, with caudal papilla (CdP) differentiated, but circle of ectodermal teloblasts (EcT) yet incomplete. E, older nauplius embryo with ventral groove (cf) in caudal papilla. F, metanauplius stage, with rudiments of first and second maxillae formed on posterior part of nauplius body before generation of teloblastic somites has begun.

1Ant, first antenna; 2Ant, second antenna; CdP, caudal papilla; EcT, ectodermal teloblasts; GD, germinal disk; I, II, first two somites; Lm, labrum; Md, mandible; 1Mx, 2Mx, first and second maxillae; Prc, procephalic lobe; Prst, prostomium; Tel, telson.

(Prst) bearing the procephalic lobes and the first antennae, a second segment (I) bearing the second antennae, a third segment (II) bearing the mandibles, and a terminal unsegmented piece (CdP), which is the caudal papilla. The embryo is now in the nauplius stage. The first segment, bearing the optic lobes and first antennae, Sollaud

claims, is the prostomium, the other two segments being the first and second true somites (*I, II*). (See also Sollaud, 1933.)

The caudal papilla of the malacostracan embryo (fig. 38 D, E, *CdP*) projects from the blastoderm. In its distal part is a circle of undifferentiated cells, ectodermal (*EcT*) and mesodermal, which are the teloblasts that will generate the postnaupliar somites. Beyond the teloblasts is the region of the telson (*Tel*) containing the anus (*An*). In its development the caudal papilla bends forward (*F*) beneath the part of the embryo contained in the blastoderm.

When the malacostracan embryo reaches the metanauplius stage there appear at the base of the caudal papilla the two maxillary somites and their appendages (fig. 38 F, *1Mx*, *2Mx*). In a study of the development of *Hemimysis*, Manton (1928) includes the two maxillary somites in the part of the body produced from the teloblasts. Sollaud (1923), however, asserts that in *Leander* both maxillary somites arise from the base of the caudal papilla before the beginning of activity in the teloblast, and that the first somite of the teloblastic series is that of the first maxillipeds. According to Sollaud, therefore, the four somites of the metanauplius (*F*), namely, those of the second antennae, the mandibles, the first maxillae, and the second maxillae, are primary somites formed directly in the primitive embryonic body between the acronal prostomium and the caudal papilla. If so, it would seem to be more than a coincidence that the same number of primary somites occurs in Malacostraca, Xiphosurida, and Trilobita.

In most of the entomostracan Crustacea the embryo hatches in the nauplius stage when only three pairs of appendages are present (fig. 4 B). The trunk is not yet distinctly segmented, but it consists of three regions. The first region is a preoral cephalic lobe bearing a median eye, the first antennae (*1Ant*), and the labrum; the second carries anteriorly the second antennae (*2Ant*) and the mandibles (*Md*), and includes posteriorly the area on which the first and second maxillae will be formed; the third region is a terminal unsegmented lobe, the telson, at the base of which is the generative zone from which will be formed the teloblastic somites. The nauplius, therefore, represents an ontogenetic stage in which the body region of the four primary somites is present, though the appendages of the posterior two of these somites are as yet undeveloped.

The crustacean nauplius has often been likened to the trochophore larva of the Polychaeta (fig. 4 A), and the two forms are comparable in so far as each represents an early stage of ontogenetic development. We cannot suppose, however, that the arthropods and the annelids

are separately derived from an ancestral form represented by the polychaete trochophore, since the adult arthropods have too many features in common with adult annelids that are not yet present in the trochophore. The common ancestor of the two groups, therefore, is to be found in a much later stage of annelid development than that of the trochophore. The trochophore and the nauplius are specialized larval forms, adapted in their general shape and structure to a temporary pelagic life; but, since they represent an early stage of phylogenetic development, and probably originated as larvae at an early phylogenetic period of evolution in their respective groups, they necessarily show primitive characters in their basic organization.

THE CEPHALIC SEGMENTATION AND THE DEVELOPMENT OF THE BRAIN

The question of the number of segments that enters into the composition of the arthropod "head" has been widely investigated and discussed, but with such lack of uniformity in the results as to lead to the suspicion that interpretation of the observed facts has been too much influenced by theoretical considerations. The writer believes that a more literal acceptance of the known facts of embryonic development in the case of the arthropod head will give a simpler and more satisfactory concept of the fundamental cephalic structure than that which has been current for several decades.

In the first place, it should be understood that there is no specific "arthropod head." The cephalic structure is a variable combination of segments, and the number of cephalized segments may be quite different in different arthropod groups, or even within a single major group. The more complex types of head, such as occur in the Mandibulata, include an anterior procephalic region bearing the labrum, the eyes, and two pairs of antennae, and a posterior gnathal region bearing the mandibles, the first and second maxillae, and in some forms the first maxillipeds or also the second maxillipeds. In the Trilobita the so-called "head" is a combination of at least four postoral somites with the prostomial acron, and the "prosoma" of the Chelicerata is a similar composite structure, except that it contains six or eight somites. On the other hand, in many of the Crustacea, the true head is a primitive structure corresponding with the procephalic part of the head in other mandibulate groups. However, differences of opinion as to the number of somites involved in the head composition pertain chiefly to the procephalic region, since the segments of the gnathal region are usually distinct in the embryo, and are readily identified by their appendages.

On the assumption that the Arthropoda and the Onychophora are derived from generalized annelids, the primary head of the onychophoran-arthropod ancestors must have been the prostomium. The prostomium, therefore, constitutes the *archicephalon* in the series of articulate animals. In the polychaete annelids the prostomium (fig. 39 A, *Prst*) supports two pairs of sensory appendages, the tentacles (*Tl*) and the palpi (*Plp*), and often a median anterior tentacle, and bears dorsally the eyes and the nuchal organs, while between it and the first somite (*I*) is situated ventrally the mouth (*Mth*). The neural elements of the prostomium, probably including originally a median apical ganglion and several paired ganglia developed in connection with the sensory organs (fig. 9 B), unite to form the composite suprapostomodal nerve mass known as the brain, or archicerebrum (*C*, *D*, *Br*).

The young arthropod embryo characteristically has at the anterior end of the body a large cephalic lobe (fig. 39 B, *Acr*). On this head lobe are developed the eyes, both simple and compound (*E*), the first antennae (*IAnt*), in some cases a pair of transient preantennal rudiments (*Prnt*), and the labrum (*Lm*). The neural elements of the embryonic head, which may include an anterior median ganglionic rudiment and as many as four paired lateral rudiments, soon unite to form the suprapostomodal brain. The exact parallelism in structure and development between the cephalic lobe of the arthropod embryo and the prostomium of the polychaete worm (A) certainly suggests a morphological identity between the two organs. In neither is there ever any external mark of segmentation, or direct evidence of the confluence of more primitive segments.

Sollaud (1923, 1933), from his study of the development of the crustacean *Leander*, contends that the embryonic head region (fig. 38 D, E, *Prst*) on which are developed the procephalic (ocular) lobes (*Prc*) and the first antennae (*IAnt*) must represent the annelid prostomium, since the first intersegmental groove runs behind the first antennae, and there is no external evidence of segmentation before it. Moreover, in the procephalic nerve ganglia, he says, only a slight constriction occurs at an early stage between the ocular, or protocerebral, parts and the antennal, or deutocerebral, parts. Sollaud asserts, therefore, that there is no valid reason for the commonly accepted view that the first antennae are homodynamous with the following appendages in the sense that they are the appendages of a primarily postoral somite that has been secondarily incorporated with the prostomium. The first antennae of *Leander*, he shows, remain uniramous, while almost from the beginning the second antennae

(D, E, *2Ant*) take on the biramous structure characteristic of the following somatic appendages. The postoral segment of the second antennae is thus, according to Sollaud's interpretation, the first true somite. The same view is strongly advocated by Holmgren (1916) and Hanström (1928) from a comparative study of the annelid and arthropod brain, but, as will be shown later, the evidence adduced by these authors from the brain structure must be qualified by facts of development.

The principal ground for the generally accepted belief that the acronal region of the arthropod embryo contains one or more "cephal-

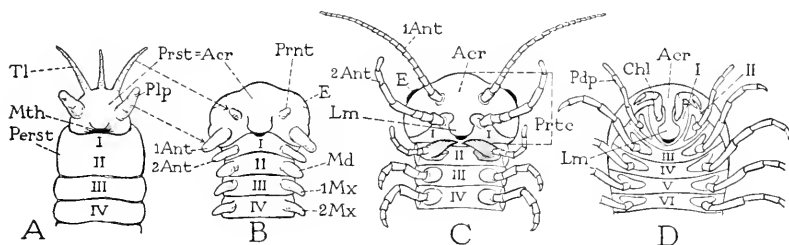


FIG. 39.—Diagrams of cephalization in the Polychaeta and Arthropoda, showing the relation of the annelid prostomium to the arthropod head on the assumption that the first antennae are prostomial appendages.

A, an adult polychaete with prostomial tentacles and palpi, first two somites united in the peristomium. B, an insect embryo in which the head (acron) is an archicephalon representing the annelid prostomium, and may bear two pairs of appendages. C, a theoretical protomandibulate arthropod, in which the head is a protocephalon (*Prtc*) composed of the acron and one somite. D, a chelicerate arthropod, in which the acron is extended laterally and dorsally over several somites united in the prosoma.

Acr, acron (arthropod prostomium); *1Ant*, first antenna (acronal appendage); *2Ant*, second antenna (appendage of first somite); *Chl*, chelicera (equivalent to second antenna); *E*, lateral eye; *I-VI*, first six somites; *Lm*, labrum; *Md*, mandible; *Mth*, mouth; *1Mx*, *2Mx*, first and second maxillae; *Pdp*, pedipalp; *Perst*, peristomium; *Plp*, palpus; *Prnt*, preantenna; *Prst*, prostomium; *Prtc*, protocephalon; *Tl*, tentacle.

lized somites" is the occurrence of temporary coelomic sacs in this region. However, it has not been shown that the presence of cavities in the cephalic mesoderm is necessarily indicative of somites, and it would seem that the burden of proof should be on the positive side of this question.

The mesoderm bands of the annelids, as shown in an earlier part of this paper, extend forward in the sides of the body from their posterior centers of propagation. In the trochophore larva the mesoderm is arrested at the mouth, but in the later development of the worm the bands extend into the prostomium and may here contain a pair of coelomic cavities. While it is usually observed that the pro-

stomial coelom of the annelids is a continuation from the coelomic cavities of the first somite, it is claimed by Binard and Jeener (1928) that the prostomial cavities of the spionid *Scolecopsis fuliginosa* belong to a distinct pair of mesodermal sacs associated with the palpi. In the Onychophora and Arthropoda the mesoderm likewise extends into the head region at the sides of, or before, the stomodaeum (fig. 41 A), and is usually excavated by a pair of well-developed coelomic sacs pertaining to the antennae (C, *AntCS*); but in the arthropods there may be formed also a pair of sacs pertaining to transitory preantennal appendages (fig. 42 B, *PrntCS*), and even a third pair in the labral region (D, *LmCS*). The position of the antennal sacs, as that of the antennal rudiments themselves, is somewhat variable in different arthropods, both structures being in some cases postoral, in others adoral, and again preoral; in the Onychophora the antennal sacs are decidedly preoral, though their posterior mesal ends embrace the stomodaeum and give rise to some of the stomodaeal muscles. The preantennal sacs are usually slightly preoral; the labral sacs lie directly before the mouth.

When we consider that the forwardly growing mesoderm bands, in their fullest development, should finally meet in front of the blastopore, it is evident that coelomic cavities formed in the cephalic region must assume adoral and preoral positions with their axes centering in the mouth (fig. 40 B). Being thus *radial* in position, the cephalic coelomic sacs cannot represent "somites" in the manner of the paired sacs lying posterior to the mouth, which are transversely opposed to each other. Hence, the assumption that these anterior sacs represent "cephalized somites" is inconsistent with the anatomical conditions that arise in the acronal region of the trunk. Moreover, as we have seen in a study of the annelids, the coelomic sacs themselves do not determine metamerism; the segmentation of the postoral parts of the mesoderm bands is secondary to metamerization of the primary somatic muscular system, and the coelomic cavities are later formed probably for physiological purposes. The coelomic sacs, therefore, correspond with the somites in the segmented part of the trunk, but similar mesodermal cavities might be formed for the accumulation of waste products in an unsegmented region such as the prostomium. The usual absence of well-differentiated coelomic sacs in the annelid prostomium, and the fact that the fullest development of the head sacs is found in the higher arthropods indicate that the formation of cavities in the cephalic mesoderm is a secondary accompaniment of advancing organization in the prostomial lobe; but the temporary

nature of the head cavities might equally suggest that they are purely ontogenetic structures, as claimed by Faussek (1899, 1901), for coelomic cavities in general.

The association of the antennal coelomic sacs with the antennae and the association of the preantennal sacs with preantennal appendicular rudiments suggest that in a primitive stage there may have

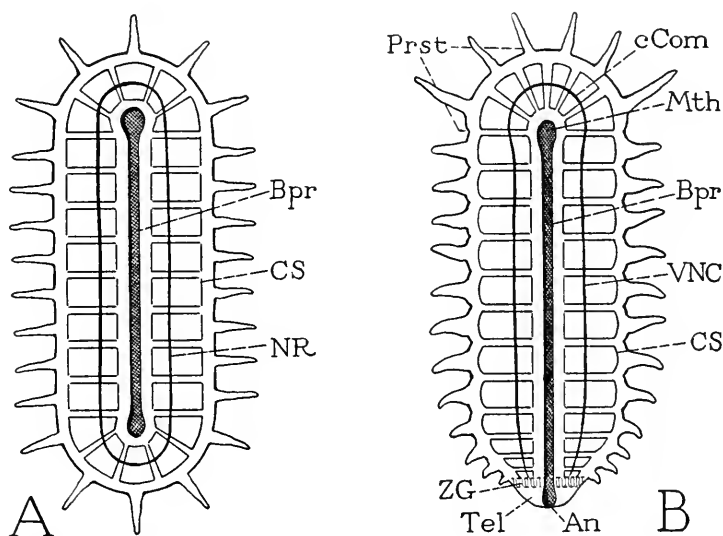


FIG. 40.—Diagrams illustrating two theories of the fundamental structure of the Articulata.

A, the theory of radial structure, based on a supposed origin of the articulata from a zoantharian polyp, according to which the coelomic sacs represent radial pouches of the enteron, and the nervous system a circumoral nerve ring, segmentation of the body being determined by the enteric pouches.

B, the theory adopted in this paper, which assumes an origin of the articulata from a creeping wormlike ancestor, based on the facts that, though the mouth is subapical, the anus is terminal, and that in embryonic development segmentation precedes the formation of the coelomic sacs, which have no connection with the enteron; the mesoderm, being teloblastic, grows forward, and, in its fullest development, may surround the mouth anteriorly, and thus give rise to a secondary radial symmetry in the prostomial region.

Bpr, blastopore; *cCom*, cerebral commissure; *CS*, coelomic sac; *Mth*, mouth; *NR*, nerve ring; *Prst*, prostomium; *VNC*, ventral nerve cord.

been a pair of appendages in the labral region corresponding with the labral sacs. Some writers have contended that the labrum itself represents a pair of united appendages, but since the labrum is immediately preoral, a pair of "labral" appendages in an annelid would arise from the base of the prostomium. Perhaps, by a long stretch of the imagination, the labral sacs might better be correlated with a hypothetical pair of primitive apical prostomial tentacles (fig. 40 B),

possibly represented by the median tentacle of certain Polychaeta (fig. 13 C), which, having a double nerve root in the brain (fig. 45 B, C, *ITINv*), might be supposed to have had itself a double origin. However, the possibility of the median polychaete tentacle having been formed by the union of a pair of apical tentacles is denied by Binard and Jeener (1928).

The theory here proposed to explain the occurrence of coelomic sacs in the prostomial region of the articulate animals has no relation whatever to the theory of Sedgwick (1884), Laneere (1926), and Binard and Jeener (1928) that the annelids and arthropods are derived from a coelenterate polyp form, and therefore have fundamentally a radial organization (fig. 40 A). A radial structure secondarily affects the anterior end of the articulate trunk because of the subapical position of the mouth (B); but the terminal position of the anus creates a quite different structure at the posterior end.

The term *acron* (Janet, 1899) is frequently used by students of arthropod embryology to designate the apical part of the arthropod head that lies anterior to the first true somite; its exact application, therefore, differs according to each writer's interpretation of the head segmentation. Janet defined the acron as the preantennal part of the head. As the term is used in the present paper, the arthropod acron is equivalent to the annelid prostomium, and is represented in the arthropod embryo by the cephalic lobe (or lobes) bearing the eyes, the labrum, the preantennae, and the first antennae. The prostomium is primarily the anterior part of the trunk not invaded by the blastopore (fig. 6 D, *Prst*); the median part of the arthropod acron is always preoral, but its lateral parts may lap backward and extend even a considerable distance behind the mouth. The *telson* at the posterior end of the trunk is not morphologically equivalent to the acron. It is traversed by the alimentary canal, and has the anus at its extremity; it does not contain coelomic sacs, but its representative in the annelids, the so-called pygidium, may support a pair of tentaclelike appendages.

The principal reasons for regarding the oculo-antennal region of the arthropod head, here defined as the acron, as representing a primarily unsegmented archicephalon corresponding with the annelid prostomium may be summarized as follows: (1) There is never any external division of the acronal region into segmental areas; (2) there is no specific evidence of the cephalization of primarily postoral somites, except in the case of the tritocerebral somite; (3) the embryonic coelomic sacs of the first antennae, the preantennae, and the labrum are formed directly where they occur in the cephalic meso-

derm, and give no evidence of having been drawn forward from behind the mouth; (4) coelomic sacs of the acronal region, so far as known, are best developed in the higher arthropods, and thus do not appear to be primitive structures; (5) the protocerebral and deutocerebral parts of the brain are always connected by preoral commissures, the only postoral cerebral commissure being that of the cephalized tritocerebral ganglia; (6) the mouth and labrum are innervated from the tritocerebral ganglia, which would not likely be the case if several other postoral ganglia preceded the tritocerebral ganglia; (7) paired appendages, sense organs, and primarily discrete nerve centers pertain both to the annelid prostomium and to the arthropod acron; (8) the first antennae of the arthropods never have

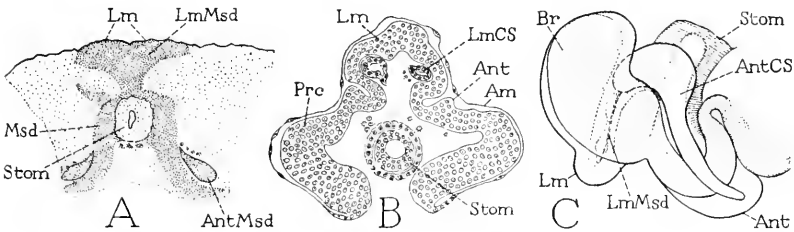


FIG. 41.—Development of the procephalic mesoderm in Orthoptera. (A, B from Roonwal, 1937; C from Wiesmann, 1926.)

A, horizontal section of anterior end of 52-hour embryo of *Locusta migratoria* Linn. showing cephalic mesoderm extending to labrum anterior to stomodaeum. B, same of 56½-hour embryo, with coelomic cavities in labral mesoderm. C, reconstruction of head of embryo of *Carausius morosus* Brunner, lateral view, with developing antennal coelom, and mesoderm extending into clypeolabral region.

Am, amnion; Ant, antenna; AntCS, antennal coelomic sac; AntMsd, antennal mesoderm; Br, brain; Lm, labrum; LmCS, coelomic sac of labrum; LmMsd, labral mesoderm; Msd, mesoderm; Prc, cephalic lobe; Stom, stomodaeum.

the structure or musculature of the following appendages; in the Crustacea they are never truly biramous.

A brief review of the facts now known concerning the development of the procephalic mesoderm and nervous system of the arthropods will show that the facts are not inconsistent with the idea that both coelomic sacs and multiple nerve centers may be formed directly in the otherwise unsegmented acronal region, and that the phenomena of embryonic development pertaining to the head are most easily understood if they are taken approximately at their face value for phylogenetic recapitulations.

The cephalic mesoderm of the arthropods is usually continuous with the mesoderm bands of the anterior somites. In a 52-hour embryo of *Locusta*, Roonwal (1937) says, "it is seen that a pair of

mesoderm bands extends upward from the junction of the head-lobe with the trunk and meet over the stomodaeum" (fig. 41 A, *Msd*). The same is true of *Carausius* (B), as shown by Wiesmann (1926), but in the crustacean *Hemimysis*, according to Manton (1928), a part of the preoral mesoderm has an independent origin from the germ band.

Among the Chelicerata the cephalic mesoderm is less developed or differentiated than in the Mandibulata. In *Limulus longispina*, as described by Kishinouye (1893), the first pair of coelomic sacs in the embryo occupies both the cephalic lobe and the cheliceral somite. Later these sacs become partially divided by an incomplete septum into a pair of cephalic sacs and a pair of cheliceral sacs, but the latter soon disappear. In the scorpion, according to Brauer (1895), the cephalic coelom is an extension of the coelomic cavities of the cheliceral somite, and is never shut off from the latter in a pair of specific head sacs. Likewise in the Pedipalpida (*Thelyphonus*) Schimkewitsch (1906) says the coelomic sacs of the head segment are continuous with those of the cheliceral segment. Kishinouye (1894) finds, on the other hand, in the Araneida (*Lycosa* and *Agelena*) a pair of coelomic sacs in the cephalic lobe that are entirely separate from the sacs of the cheliceral somite. The cephalic sacs are later divided each into two parts; the ventral sections disappear, the dorsal sections elongate upward and form between them the cephalic aorta.

In the Mandibulata coelomic cavities associated with the first antennae are of common occurrence in the cephalic mesoderm. A diverticulum from each antennal sac extends into the corresponding antenna (fig. 41 C, *AntCS*) and gives rise to the antennal musculature. The inner dorsal parts of the sacs, as observed by the majority of investigators (see Wiesmann, 1926, Roonwal, 1937), grow mesally into the space between the stomodaeum and the brain, where they extend anteriorly and posteriorly and form the cephalic part of the aorta, including the anterior end of the tubular aorta proper, and an open distributing section that extends from beneath the brain to the clypeal region. The cephalic aorta of the crustacean *Hemimysis*, however, is said by Manton (1928) to be a product of the preantennal mesoderm.

The presence of preantennal coelomic sacs associated with small evanescent rudiments of preantennal appendages (figs. 42 A, 43 A, *Prnt*) is recorded by Heymons (1901) in *Scolopendra* (fig. 42 B, *PrntCS*), and by Wiesmann (1926) in *Carausius* (F, *PrntCS*), and the occurrence of coelomic cavities in the preantennal mesoderm of *Hemimysis* is reported by Manton (1928), though vestiges of pre-

antennal appendages are not known in the Crustacea. In the diplopod *Platyrhacus amauros*, Pflugfelder (1932a) shows that a pair of coelomic sacs is formed in the cephalic lobes of the embryo in con-

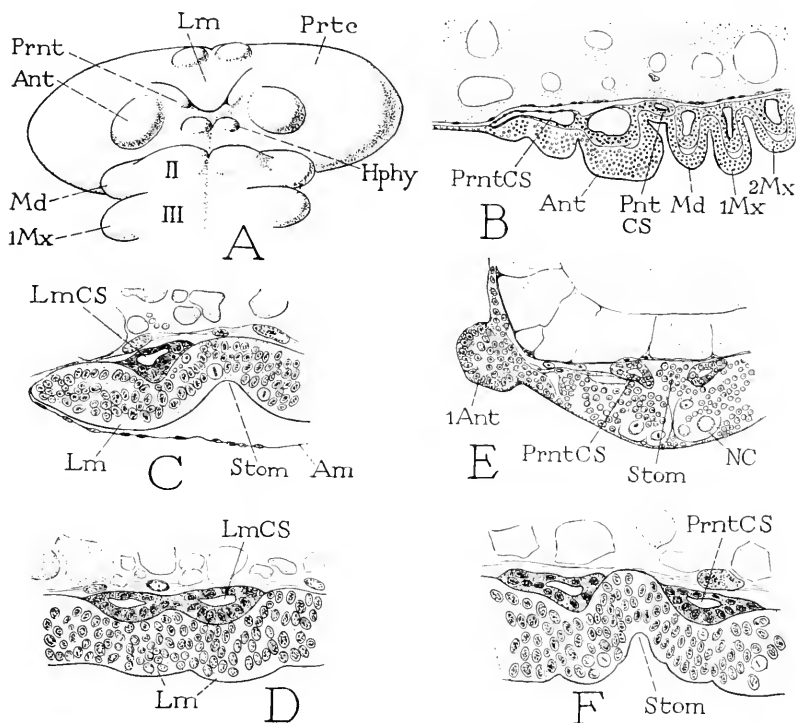


FIG. 42.—Embryonic appendages and coelomic sacs of the procephalic region of an insect, a chilopod, and a crustacean.

A, head (protocephalon) and two following somites of young embryo of *Carausius morosus* Brunner, ventral view (from Wiesmann, 1926). B, lengthwise section through cephalic appendages and coelomic sacs of embryo of *Scolopendra* (from Heymons, 1901). C, lengthwise section through a coelomic sac of the embryonic labral rudiment of *Carausius* (from Wiesmann, 1926). D, cross-section of same through labral coelomic sacs (from Wiesmann, 1926). E, cross-section through preantennular coelomic sacs of embryo of *Hemimysis lamornae* (from Manton, 1928). F, cross-section through preantennal coelomic sacs of embryo of *Carausius* (from Wiesmann, 1926).

Am, amnion; Ant, first antenna; Lm, labrum; LmCS, labral coelomic sac; Md, mandible; 1Mx, 2Mx, first and second maxillae; PntCS, postantennal coelomic sac; Prnt, preantenna (preantennule); PrntCS, preantennal (preantennular) coelomic sac; Prtc, protocephalon (acron and first somite); Stom, stomodaeum.

nection with the protocerebral lobes of the brain (fig. 44 D, *Pcr*), and a second pair in connection with the deutocerebral lobes (*Dcr*). Hence, if there is any necessary homology between the cavities of the cephalic mesoderm in different arthropods, the "protocerebral"

sacs of *Platyrrhacus* should represent the preantennal sacs of *Scolopendra*, *Carausius*, and *Hemimysis*, though there are in the diplopod, as in the crustacean, no corresponding appendage rudiments. While, in most cases observed, the preantennal mesoderm is a part of the general mesoderm, the preantennal mesoderm of *Hemimysis* is said by Manton (1928) to have an independent origin from the germ band just behind the optic lobes. When the arms of the V-shaped germ band of *Hemimysis* later come together, the preantennal mesoderm rudiments are approximated immediately before the mouth. In their growth, Manton says, they extend posteriorly and embrace the lateral and dorsal walls of the stomodaeum, their cavities entirely disappear, and their walls give rise to a part of the stomodaeal ("stomach") muscles, and to the cephalic aorta.

Coelomic sacs of the labral region of the embryonic head were first described by Wiesmann (1926) in the stick insect, *Carausius morosus*, and have since been observed by Mellanby (1936) in the hemipteron *Rhodnius*, and by Roonwal (1937) in a grasshopper, *Locusta migratoria*. Pflugfelder (1932a) describes in the diplopod *Platyrrhacus* a pair of mesodermal cavities in the "clypeus" (fig. 44 D, *Clp*), but since these cavities lie immediately before the mouth, they evidently correspond with those called "labral" in the insects. In both *Locusta* (fig. 41 A) and *Carausius* (C) the head mesoderm extends into the labrum (*LmMsd*) anterior to the stomodaeum (*Stom*), and the cavities formed in it are thus literally preoral in position (fig. 42 C, *LmCS*); the mesal walls of the labral sacs of *Carausius* are united before the mouth (D). In *Locusta*, Roonwal says, the labral and stomodaeal mesoderm is loosely continuous prior to the appearance of the labral cavities (fig. 41 A), but when the sacs are formed the latter are independent structures (B, *LmCS*). After the disappearance of the cavities the coelomic cells remain as two bodies of mesoderm that suggest similar mesodermal masses found in the labrum of certain other insects in which corresponding cavities are not known to occur.

The definitive brain of the mandibulate arthropods consists of an anterior bilobed part, including the protocerebrum and the deutocerebrum, which innervate respectively the eyes and the first antennae, and of a pair of posterior lobes, the tritocerebrum, which innervate the second antennae when these appendages are present. The proto-deutocerebral lobes are always united above the stomodaeum, and thus appear to belong to the prostomial part of the head; the tritocerebral lobes, on the other hand, are unquestionably derived from the postoral somite of the second antennae, and are connected by a

postoral commissure. In many cases the dorsal lobes are developed in the embryo from a single pair of generative centers in the ectoderm, just as are the corresponding lobes of the brain in the Onychophora and in some of the Annelida. Considering, however, that the annelid brain, as shown in the larva of *Lopadorhynchus*, has probably taken its origin from a number of discrete prostomial ganglionic centers corresponding with the sensory organs of the prostomium, we should expect that a more primitive condition in the arthropods would show that the definitive brain of these animals is likewise a composite structure formed by the union of primarily

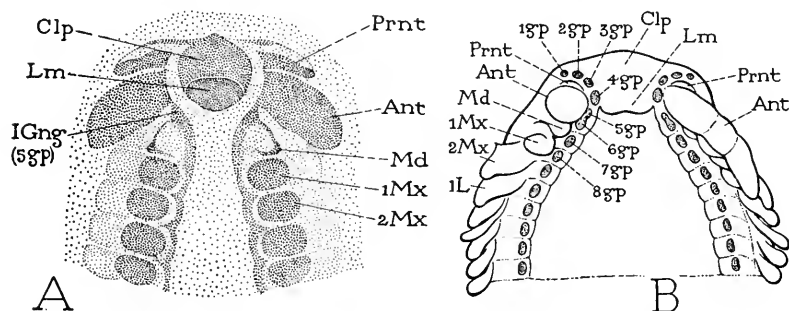


FIG. 43.—Embryonic development of the cephalic appendages and nerve ganglia of a chilopod, *Scolopendra*. (From Heymons, 1901.)

A, anterior end of germ band with rudiments of appendages, including preantennal, antennal, mandibular, and maxillary lobes, but no rudiments of postantennal (intercalary) appendages, though postantennal (tritocerebral) somite marked by a pair of ganglia (*IGng*). B, same, later stage (antenna removed on left), showing ganglionic pits (*gp*) of ectoderm from which ganglia are developed.

Ant, antenna; *Clp*, clypeus; *1gp*, generative pit of optic ganglion; *2gp*, pit of protocerebral ganglion; *3gp*, pit of preantennal ganglion; *4gp*, pit of antennal ganglion; *5gp*, pit of tritocerebral ganglion; *6gp-8gp*, pits of mandibular and maxillary ganglia; *IGng*, tritocerebral ganglion; *1L*, first leg; *Lm*, labrum; *Md*, mandible; *1Mx*, *2Mx*, first and second maxillae; *Prnt*, preantenna.

separate ganglia. Various studies on the development of the arthropod brain, in fact, demonstrate its diffuse origin.

The best-known example of the development of the arthropod brain from diffuse ganglionic centers is that described by Heymons (1901) in *Scolopendra*. The embryonic cephalic appendages of *Scolopendra* that correspond with cerebral rudiments include the persistent antennae (fig. 43 A, *Ant*) and a pair of transient preantennae (*Prnt*), appendages of the postantennal "intercalary," or tritocerebral, somite being absent. The definitive brain of *Scolopendra*, according to Heymons, is formed by the coalescence of an anterior unpaired ganglionic rudiment and five paired rudiments. The unpaired rudiment arises

directly from the ectoderm of the clypeal region of the cephalic lobes (fig. 43 B, *C1p*), and appears before any of the appendages except the antennae are formed. The paired rudiments are groups of ganglionic cells proliferated from the inner ends of small ectodermal pits (*1gp-5gp*). The first of these rudiments to be formed (*2gp*) lie at the extremities of the median rudiment, and their cells become closely associated with the latter to produce a cellular mass that becomes the lamina dorsalis of the definitive protocerebrum. Laterad of these rudiments are formed a pair of pits (*1gp*) that furnish principally the cells of the definitive frontal lobes of the brain, and later when the eyes appear give rise also apparently to the small optic lobes. Following the lateral rudiments of the lamina dorsalis on each side are formed in series three other cephalic pits, which generate respectively the primitive ganglionic centers of the preantennae (*3gp*), of the antennae (*4gp*), and of the appendageless tritocerebral somite (*5gp*). The two series of neurogenic pits are continued posteriorly on the mandibular, the maxillary, and the leg somites.

Heymons regards the median unpaired brain rudiment as the equivalent of the annelid "archicerebrum," but it would seem rather to correspond with the ganglion of the apical plate of the polychaete larva. The two paired rudiments that combine with the median rudiment to form the definitive protocerebrum he refers also to the "acronal," or prostomial, part of the head, but the preantennal, antennal, and tritocerebral rudiments he claims represent postoral somites. The preantennal ganglia constitute at first a connection between the protocerebrum and the deutocerebrum, but later they merge so completely into the brain that their identity is lost in the definitive brain structure. The deutocerebral lobes formed of the antennal ganglia lie primarily behind the protocerebrum, but with the forward migration of the antennae they become transposed to a position anterior to the protocephalon and take on a conical form with the antennal nerves issuing from their distal ends. The tritocerebral lobes lie beneath the deutocerebral lobes and are continuous with the stomodaeal connectives.

The claim of Heymons that the preantennal and antennal ganglia represent postoral somites is not substantiated by any external evidence of segmentation in the corresponding cephalic region of the scolopendrid embryo, and as represented in Heymons' figure (fig. 43 B) these ganglia appear to be actually preoral in position. In none of the arthropods do the true cerebral ganglia have postoral commissures, but the preoral position of their commissures in the brain mass, Heymons says, is to be explained ontogenetically by the

fact that the commissures are not formed until after the respective ganglia have taken a preoral position. This proposed explanation, however, is merely the statement of a fact that can as well be taken as evidence that the ganglia themselves are morphologically preoral.

In the Diplopoda the embryonic rudiments of the nervous system appear to be completely double, for no median ganglionic center has been observed corresponding with the "archicerebral" rudiment described by Heymons in *Scolopendra*. Preantennal appendages are absent so far as known, and the tritocerebral somite always lacks appendages, as in the Chilopoda. According to Robinson (1907) the nervous system of a 16-day-old embryo of *Archispirostreptus* consists of a pair of trilobed "archicerebral" rudiments situated before the mouth (fig. 44 E, *Arc*), and of two ganglionated nerve cords proceeding posteriorly from the latter around the stomodaeum. The first ganglia of the cords (*AntGng*), which are distinctly postoral, Robinson claims are the antennal ganglia. The next pair, she says, are the ganglia of the tritocerebral somite (*TcrGng*), which has no appendages, and the next pair (*MdGng*) belong to the mandibles. At a later stage (F), just before hatching, the "antennal ganglia" (*AntGng*), to which Robinson says the tritocerebral ganglia are now joined, still lie behind the mouth and are approximated to the median line. It is very surprising, however, that antennal ganglia should be postoral at such a late stage of development, and not yet united with the protocerebrum, so much so, in fact, that the relation of these alleged "antennal" ganglia to the antennae becomes questionable. Robinson gives no evidence of any nerve connection between the ganglia and the antennae (*Ant*); hence we might suspect that the antennae are innervated from the posterior ganglia of the "archicerebral" groups (*Arc*), and that the first postoral ganglia are the tritocerebral ganglia.

Heymons (1897) gives a brief description of the embryo of *Glomeris* (fig. 44 C), in which the antennae (*Ant*) appear as adoral appendages of the cephalic lobes (*Prc*), whence presumably they derive their innervation.

A more detailed account of the cephalic and cerebral segmentation of a diplopod is given by Pflugfelder (1932 a) for *Platyrhacus amauros*, but it only adds to the difficulties of understanding the development and morphology of the diplopod head. According to Pflugfelder, the protocerebral and deutocerebral elements of the brain appear on the surface of the young embryo of *Platyrhacus* as a single pair of preoral cephalic lobes (fig. 44 A, *Prc*). Just behind the mouth is the somite of the antennae (*Ant*), and the latter is

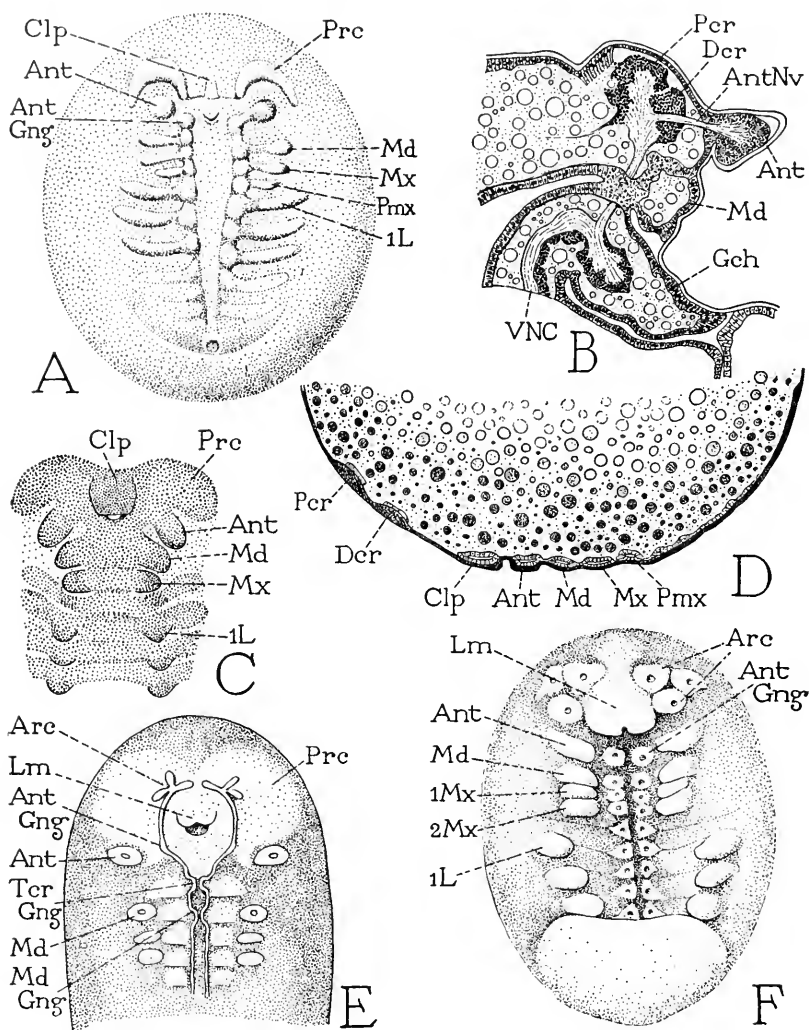


FIG. 44.—Embryonic segmentation of the head of Diplopoda as interpreted by different investigators.

A, germ band of *Platyrhacus amauros* Attems before invagination (from Pflugfelder, 1932 a). B, longitudinal section of head of embryo of *Platyrhacus amauros* shortly before hatching (adapted from Pflugfelder, 1932 a). C, young embryo of *Glomeris* (from Heymons, 1897). D, longitudinal section of germ band of *Platyrhacus amauros* just before invagination, showing preoral coelomic sac of clypeal region and sacs of four postoral somites (from Pflugfelder, 1932 a). E, embryo of *Archispirostreptus* sp., about four days before hatching (from Robinson, 1907). F, same, one day before hatching (from Robinson, 1907).

Ant, antenna; AntGng, antennal ganglion; AntNv, antennal nerve; Arc, archicerebrum; Clp, clypeus (labrum); Der, deutocerebrum; Gch, gnathochilarium; 1L, first leg; Md, mandible; MdGng, mandibular ganglion; Mx, maxilla; 1Mx, 2Mx, first and second maxillae; Pcr, protocerebrum; Pmx, postmaxillary appendage, or somite; Prc, procephalic lobe; TcrGng, tritocerebral ganglion; VNC, ventral nerve cord.

followed directly by the mandibular (*Md*) and two maxillary somites (*Mx*, *Pmx*), there being no evidence of a tritocerebral somite. In sections the cephalic lobes show internally a distinct division into a protocerebral rudiment (*D*, *Pcr*) and a deutocerebral rudiment (*Dcr*), each later accompanied by a coelomic sac. It would seem to be inferred from Pflugfelder's description, though not so stated, that the primary antennal ganglia lie in the postoral "antennal somite" (*Ant*), and yet he says, "das Deutocerebrum tritt sehr früh mit den Antennen in Verbindung durch den Antennennerv," and he clearly shows the antennal nerve connection with the preoral deutocerebrum (*B*,

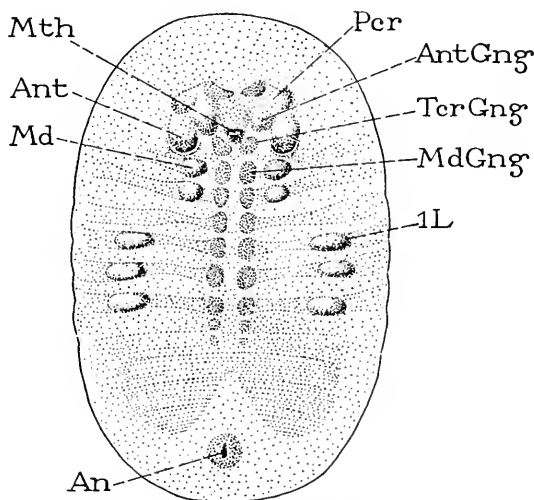


FIG. 44 G.—Germ band of a diplopod, *Archispirostreptus gigas* Peters, showing rudiments of appendages and ganglia. (From Silvestri, 1933.)

An, anus; *Ant*, antenna; *AntGng*, antennal ganglion; *1L*, first leg; *Md*, mandible; *MdGng*, mandibular ganglion; *Mth*, mouth; *Pcr*, protocerebrum; *TcrGng*, tritocerebral ganglion.

AntNv). The anatomical evidence here would seem to show that the true morphological relations of the antennae are with the deutocerebral ganglia, and we can only suppose, therefore, as in the case of Robinson's account of *Archispirostreptus*, that the postoral so-called "antennal" ganglia are the tritocerebral ganglia. In any event, the implication from Pflugfelder's statements that the antennae are appendages of a postoral somite, but are finally innervated from the preoral deutocerebrum gives the impression that there is some error involved.

The interpretation of the anterior cephalic ganglia of the diplopod embryo given by Silvestri (1933), illustrated in *Archispirostreptus gigas* (fig. 44 G), unquestionably presents the most reasonable view

that can be taken concerning the homologies of the ganglionic rudiments, since it disposes of the latter in a manner entirely consistent with the evident facts in other arthropods. According to Silvestri the ganglia of the antennae (*AntGng*) are neural masses situated mesad of the antennal bases, and the first pair of postoral ganglia (*TcrGng*) are the tritocerebral ganglia (ganglia of the intercalary somite). It should be observed that the antennal ganglia, as shown by Silvestri, have a preoral position and are not separated from the protocerebral lobes of the brain (*Pcr*).

Among the higher arthropods the more primitive stages in the brain development are generally not shown in embryonic recapitulation, for the proto-deutocerebral centers are usually proliferated from the ectoderm as a unified ganglionic cell mass, just as in the Onychophora and in many of the Annelida. It is observed by Baden (1936) and by Roonwal (1937), however, that the brain of the grasshopper (*Melanoplus*, *Locusta*) is formed from five pairs of ganglionic centers, three of which give rise to the protocerebrum and the optic lobes, and the other two to the deutocerebrum and the tritocerebrum, respectively. On the other hand, Nelson (1915) finds that in the honey bee the lateral surfaces of the primarily undivided cephalic lobes of the embryo become directly differentiated into three areas from which are proliferated the neural centers of the protocerebrum, the deutocerebrum, and the tritocerebrum.

In view of the well-authenticated examples of a diffuse origin of the cerebral ganglionic centers in the arthropods, the theory of Holmgren (1916) and of Hanström (1928) that the protocerebrum and the deutocerebrum are secondarily differentiated parts of a primitive, undivided archicerebrum does not appear to be substantiated by the facts of embryogeny. However, since the definitive brain is evidently a conglomerate of primitively separate ganglionic centers in the Annelida as well as in the Arthropoda, the general contention of these authors is not invalidated, namely, that both the protocerebral and the deutocerebral parts of the arthropod brain belong to the preoral prostomial region of the head, and, therefore, together represent the annelid archicerebrum.

The concept that all coelomic sacs and corresponding nerve centers represent postoral somites seemed reasonable enough, as applied to the arthropod head, when only antennal sacs were known; it was somewhat stretched, though still acceptable, when preantennal sacs were discovered; but now that we must add a third pair of cephalic sacs lying directly before the mouth in the labral region it begins to look farfetched. The theory here proposed, illustrated at D of

figure 45, accepts the embryonic facts more literally. It assumes that the archicephalic nervous system of the arthropods, as that of the annelids, has been built up from groups of ganglionic cells centering

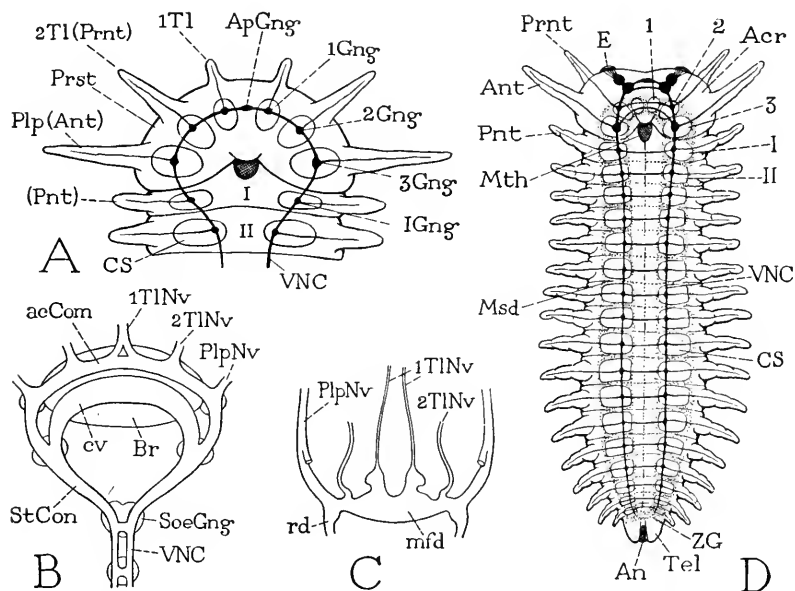


FIG. 45.—Suggestions of homologies between the prostomium of the annelids and the acronal region of the arthropod head.

A, diagram of the anterior segments of a theoretical "lobopod" annelid, with elemental ganglia corresponding with those of the arthropod cerebrum distributed on a preoral commissural arch of the nerve cords, and the potential number of coelomic sacs of the arthropod acron shown in their possible relation to the prostomial appendages. B, diagram of the fundamental structure of the prostomial nervous system of a polychaete annelid (from Binard and Jeener, 1928). C, reconstructed frontal section of dorsal fibrillar mass of brain and nerves arising from it in a sedentary polychaete, *Sabellaria spinulosa* Leuckart (from Binard and Jeener, 1928). D, analytical diagram of the relation of the coelomic sacs of an arthropod to the central nerve ganglia and the associated appendages.

acCom, anterior cerebral commissure; *Acr*, acron (prostomium); *An*, anus; *Ant*, antenna; *ApGng*, apical ganglion; *Br*, brain; *CS*, coelomic sac; *cv*, ventral fibrillar mass of brain; *E*, lateral eye; *1Gng*, protocerebral ganglion; *2Gng*, preantennal ganglion; *3Gng*, antennal ganglion; *I*, *II*, first and second somites; *1Gng*, first somatic (tritocerebral) ganglion; *mfd*, dorsal fibrillar mass of brain; *Msd*, mesoderm; *Mth*, mouth; *Plp*, palpus; *PlpNv*, palpal nerve; *Pnt*, postantennal appendage; *Prnt*, preantenna; *Prst*, prostomium; *rd*, dorsal root of stomodaeal connective; *SoeGng*, suboesophageal ganglion; *StCon*, stomodaeal connective; *Tel*, telson; *1Tl*, first tentacle; *2Tl*, second tentacle; *1TlNv*, nerve roots of median tentacle; *2TlNv*, nerve of second tentacle; *VNC*, ventral nerve cord; *ZG*, zone of growth; *1*, labral coelomic sac; *2*, preantennal coelomic sac; *3*, antennal coelomic sac.

upon a fibrous commissural tract arched forward around the mouth and continuous posteriorly with the ventral nerve cords of the somatic system. The primary cephalic ganglia included a median anterior

ganglion, paired protocerebral and optic ganglia, paired preantennal ganglia, and paired first antennal ganglia. That these ganglia belong to the preoral acron (*Acr*) is shown by the fact that the paired ganglia are always connected by preoral commissures. The cephalic mesoderm extends forward from the somatic mesoderm bands, and, in its fullest development, surrounds the mouth anteriorly; it may become excavated by cavities corresponding with the first antennae (3), the preantennae (2), and the labrum (1). The development of the prostomial nerve ganglia and mesodermal cavities is determined probably in all cases by external structures (appendages or sense organs), but the acronal neuromeres and coelomic sacs, because of their radial position around the mouth, cannot have the same relation in the body structure as have their postoral counterparts that are transversely opposed to each other. For a like reason there is no prostomial metamerism of the muscular system. The same concept may be applied to the preoral lobe of the polychaete annelids (*A*), assuming that potentially the annelid prostomium might have a full quota of coelomic sacs corresponding with its appendages, which actually it does not have. The tritocerebral somite of the arthropods thus represents the first postoral somite of the annelids. The tritocerebral ganglia are secondarily united with the preoral cerebrum in the Onychophora and in most of the Arthropoda, and always have a postoral commissure; the corresponding appendages are the jaws of the Onychophora, the chelicerae of the Chelicerata, and the second antennae of the Mandibulata.

The definitive arthropod brain more closely resembles the brain of the Polychaeta than that of the Onychophora. Its principal part is the protocerebrum, formed of a median apical ganglion and the first pair of lateral ganglia, with which are connected the optic ganglia. The preantennal ganglia lose their individuality in the general cerebral mass. The antennal ganglia form the deutocerebral lobes, but the latter take a forward position beneath the protocerebrum, with the result that, in the definitive condition, the antennal nerves arise anteriorly *below* the optic lobes. In the Onychophora, on the other hand, though the antennae are anterior, the brain maintains a horizontal position (fig. 25 A, C) with the antennal commissure behind the optic region, and the antennal tracts (*AntT*) traverse the dorsal part of the brain *above* the optic lobes. The tritocerebral ganglia are united with the primary cerebrum in the Onychophora and in nearly all the Arthropoda, but the union would seem to have taken place separately in the two groups, since in some of the lower Crustacea the corresponding centers are independent ganglia on the nerve cords, as they are in most of the Annelida.

EVOLUTION OF THE HEAD

The prostomial acron does not constitute the definitive head of any known arthropod; there is always added to the acron at least one postoral somite, and generally the definitive head includes from four to six somites. A head composed of the acron and one somite, however, recurs so frequently, either in the adult stage or in ontogenetic development, as to suggest that a simple head structure of this kind (fig. 39 C, *Prtc*) represents the earliest stage in the evolution of the more complex types of arthropod head. It may hence be termed the *protocephalon*. The best example of a functional protocephalon is to be seen in the anostracan Branchiopoda (fig. 50 A), in which the definitive head is a large cephalic lobe (*Prtc*) bearing the eyes, both pairs of antennae, and the labrum. The protocephalon is unquestionably the primitive head of all the mandibulate arthropods. There is no direct evidence, however, that it ever occurred as a specific stage in the evolution of the Trilobita or the Chelicerata, and hence, in the ancestors of these groups, and in the protarthropods generally, the primitive head may have been merely the prostomial acron.

Crampton (1928) applies the term "archicephalon" to a supposed stage in the cephalic evolution of the arthropods when the head consisted of the procephalic region and the mandibular somite. That such a stage occurred relatively late in the phylogenetic history of the head, however, is clearly shown in the ontogeny of the Mandibulata, in which the primitive embryonic head is always a cephalic lobe bearing the first antennae and usually including the second antennal somite, while the gnathal somites are still a part of the body region. Antedating this protocephalic stage, however, there must theoretically have been a truly primitive stage when there was no head structure other than the prostomium. The prostomium, therefore, which becomes the acronal region of the definitive head, is the only stage in the evolution of the arthropod head that might properly be termed the "archicephalon."

The trilobite branch of the protarthropods is characterized by a lateral expansion of the body, produced by an extension of the lateral margins of the tergal plates into long flat lobes (fig. 36 E, 48 D). The dorsal surface of the body thus presents a median elevated area (rhachis) accommodating the alimentary canal, and broad depressed lateral areas (pleurae). On the under surface the true venter (fig. 48 D, *V*) is the area between the leg bases, the areas laterad of the legs being the ventral doublure (*dbl*) of the dorsum. The appendages bear long coxal epipodites (*Eppd*) supporting branchial lamellae or filaments.

The so-called "head" of an adult trilobite (fig. 36 H, *H*), as we have seen, represents the 5-segmented body of the larva (*A*), the "body" segments of the adult being formed secondarily of a series of teloblastic somites generated from a subterminal zone of growth (*ZG*). The very young larva (fig. 46 *A*) presents a broad anterior acronal region (*Acr*), and a postacronal region in which are already differentiated the elevated median glabella (*glb*), which is the cephalic part of the rhachis, and the broad lateral areas (*fg*) that become the fixed cheeks of the adult (*E*). When the glabellar impressions appear (*B*, *C*) the glabella is cut into five consecutive divisions, but it is evident that the first division, or frontal lobe (*C*, *frl*), is derived from the acron, and that the following four divisions represent the first four postacronal somites (*I-IV*). With successive stages of development (*B*, *C*, *D*), the lateral wings of the acron (*lg*) extend posteriorly along the sides of the somites and eventually form the so-called free cheeks of the adult (*E*, *lg*), on which are located the compound eyes (*E*). The cephalic segmentation of the trilobite larva, therefore, may be represented as at *I* of figure 46, in which the intersegmental lines (*Is-4s*) are theoretically extended to the lateral margins of the body. A median dorsal ocellus, when present, is always situated on the glabella, but since it must belong to the acron, it is placed on the frontal lobe in the diagram (*I*, *dO*).

In the mature trilobite head of typical structure (fig. 46 *E*), the preocular part of the acronal suture (*I*, *Is*) has disappeared, but the postocular parts become the posterior parts of the sutures known as the "facial sutures" (*fsp*), the preocular parts of which (*fsa*) are probably secondary lines of cleavage developed to facilitate moulting. In some forms the facial sutures end on the lateral margins of the head; in others they go to the posterior margin (*E*), and in such cases the genal spines are continuations of the free cheeks. On the ventral surface of the head (*F*) the acronal surface is broadly inflected to form the doublure (*dbl*), which carries the labrum (*Lm*), or "hypostome," on its preoral margin. The probable dorsal segmentation of the adult trilobite head, therefore, may be represented diagrammatically as shown at *J* of figure 46. The acron (*Acr*) clearly forms an extensive part of the mature cephalic structure, since it must include the frontal lobe of the glabella (*frl*), the free cheeks (*lg*) with the compound eyes (*E*), and the doublure (*F*, *dbl*) with the labrum (*Lm*). Furthermore, since the dorsal ocellus often occurs far back on the glabella (*J*, *dO*), we must assume that it is contained in a median tongue of the frontal lobe extended posteriorly into the glabellar somites, because the simple eyes as well as the compound eyes always belong to the acronal segment.

The antennal appendages of the trilobites, judging from their filamentous form in contrast with the segmented structure of the following appendages, evidently represent the first antennae (anten-

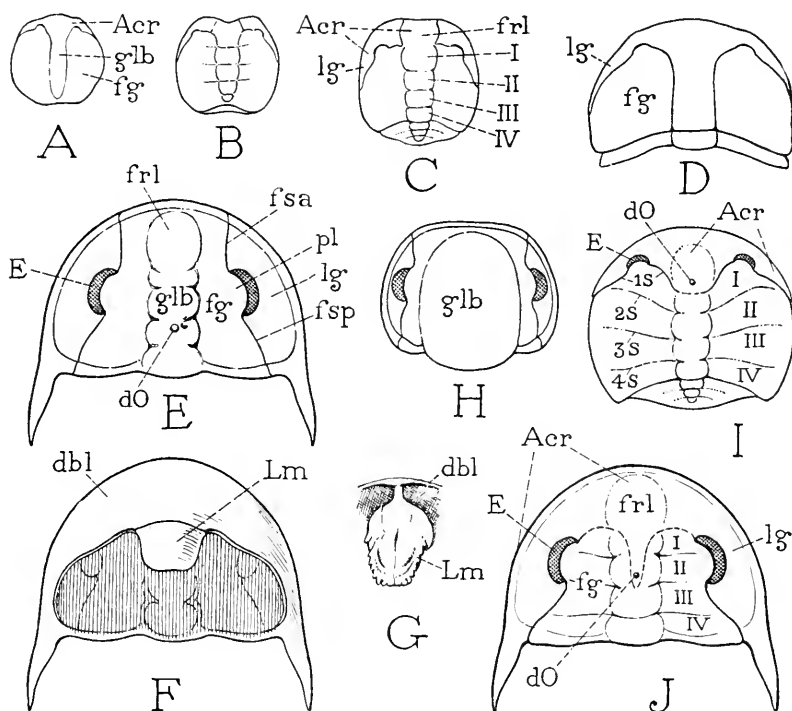


FIG. 46.—Segmentation of the trilobite "head," or prosoma.

A-D, four consecutive stages in the larval development of *Blainia gregaria* Walcott, showing gradual posterior extension of lateral wings (free cheeks) of acron against sides of anterior somites, and division of glabella (C) into four segmental areas behind frontal lobe of acron (from Lalicker, 1935). E, diagram of typical trilobite head, dorsal surface. F, diagram of ventral surface of trilobite head, showing labrum attached to margin of doublure. G, labrum of *Paedeumias transitans* Walcott, example of a stalked labrum (from Walcott, 1910). H, head of *Holotrachelus punctiliosus*, with segmentation obliterated in the large swollen glabella (from Warburg, 1925). I, diagram of larval trilobite, with head segmentation indicated. J, head of adult trilobite with probable segmentation deduced from the larval structure (I).

Acr, acron; *dbl*, doublure; *dO*, dorsal ocellus; *E*, compound eye; *fg*, fixigene (fixed cheek); *frl*, frontal lobe (of acron); *fsa*, anterior part of facial suture; *fsg*, posterior part of facial suture; *glb*, glabella; *I-II'*, cephalic somites; *lg*, librigena (free cheek); *Lm*, labrum; *pl*, palpebral lobe; *1s-4s*, intersegmental sutures of head.

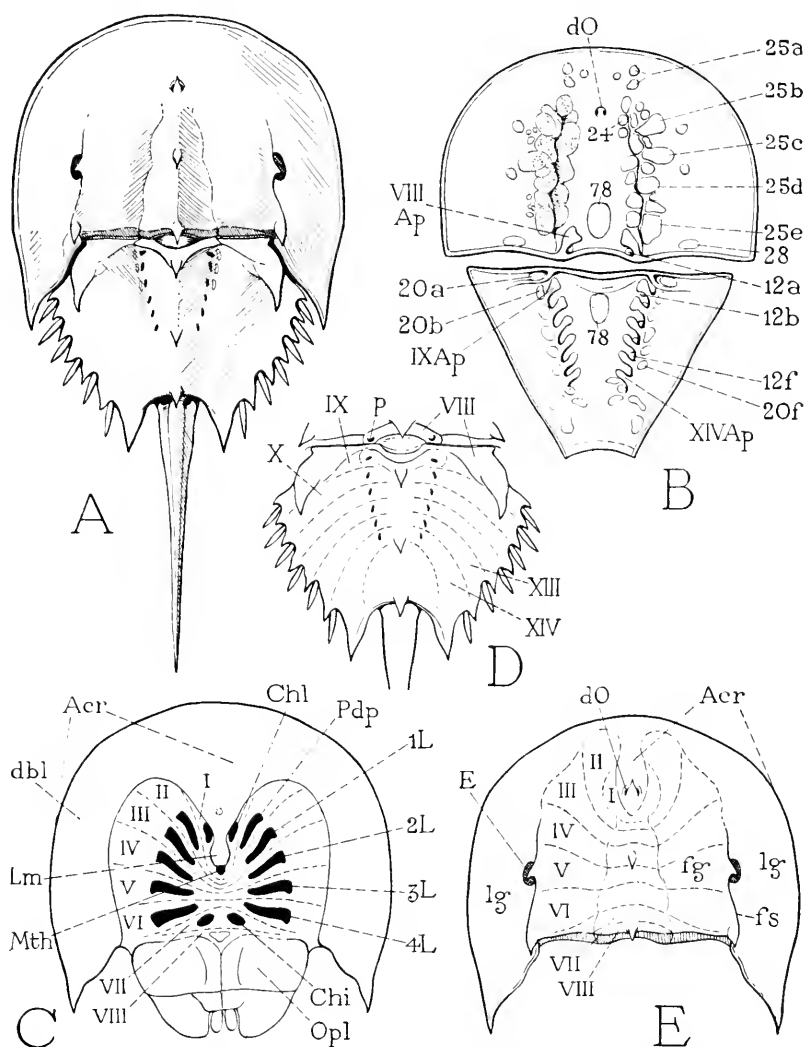
nules) of other arthropods; if so, according to the theory here followed, they should belong to the acron, and perhaps had their muscle attachments on the frontal lobe. The position of the antennal

bases is not exactly known, but the antennal appendages are generally represented as arising at the sides of the labrum. The four following segmented, leglike appendages of the head clearly pertain to the four postfrontal somites of the dorsal shield.

Henriksen (1926), in his analysis of the segmentation of the trilobite head, convincingly argues that the free cheeks bearing the compound eyes must belong to the "eye segment" (acron), and that the preocular parts of the facial sutures are secondary lines of cleavage to facilitate moulting; but the median part of the eye segment he believes is represented only by the narrow anterior marginal rim of the dorsal shield before the frontal lobe. Henriksen notes, however, the anomalous position of the median eye far back on the glabella, and it is not clear why the reasoning by which he assigns the free cheeks to the eye segment does not demand that the eye segment include also the area of the median eye. The antennae, Henriksen contends, belong to a separate postoral somite, represented dorsally by the frontal lobe of the glabella. Furthermore, since he believes that the trilobite head must have the same segmentation as the head of certain Crustacea, Henriksen concludes that a second antennal somite has been lost by the trilobites. To the writer this theoretical elaboration of the trilobite head to give conformity with crustacean structure appears quite unnecessary, since the trilobites are non-mandibulate arthropods having no immediate relations with the Crustacea, and their structure clearly leads into that of the Chelicerata.

The Xiphosurida, in the structure of the prosoma, show unmistakably their trilobite derivation, for the trilobite head is carried over into the xiphosurid prosoma with few changes other than the inclusion of a few extra segments, the loss of the antennae, and a differentiation of the other appendages.

A comparison of figure 47 A with figure 46 E will show at once the likeness of the prosomatic carapace of *Limulus* to the typical head shield of a trilobite. The segmentation of the xiphosurid prosoma is evident from the position of the limb bases on the ventral surface (fig. 47 C), where it is seen that the anterior somites lap forward at the sides of the labrum from behind the central mouth, while the posterior somites curve somewhat backward. The chelicerae (*Chl*) thus come to have anatomically a preoral position at the sides of the labrum, though their somite (*I*) is morphologically postoral, and the same is true of the pedipalps (*Pdp*) and the first legs (*1L*). On the inner surface of the prosomatic carapace the attachments of the limb muscles (fig. 47 B), as depicted by Benham (1885), follow the segmentation indicated ventrally by the limb bases. The chelical

FIG. 47.—Segmental analysis of Xiphosurida (*Limulus polyphemus* Linn.).

A, young adult, dorsal surface. B, ventral surface of dorsal carapace, showing muscle attachments and series of dorsal apodemes, or entapophyses (from Benham, 1885, with dorsal ocelli added). C, ventral surface of prosoma, showing segmentation as indicated by position of leg bases. D, dorsal surface of opisthosoma, with segmentation indicated. E, theoretical approximate segmentation of prosoma.

Acr, acron; *Ap*, tergal apodemes (entapophyses); *Chi*, chilarium; *Chl*, cheliceræ; *dbl*, doublure (ventrally inflected part of acron); *dO*, dorsal ocellus; *E*, compound eye; *fg*, fixigene; *fs*, facial suture; *I-XIV*, postoral somites; *L*, leg; *lg*, librigenæ; *Lm*, labrum; *Mth*, mouth; *Opl*, genital operculum; *p*, external pits of tergal apodemes; *12a, b, f*, dorsal attachments of tergo-sternal muscles of opercular and gill somites; *20a, b, f*, dorsal attachments of anterior muscles of opercular and gill appendages; *25a-e, 28*, dorsal attachments of tergo-coxal muscles of prosomatic appendages.

muscles (24) arise near the midline just behind the dorsal eyes; the muscles of the pedipalps (25a) take their origins farthest forward; and the muscles of the other appendages (25b-25c) are distributed on the following areas of the "fixed cheeks." Diagrammatically, therefore, we may represent the segmentation of the prosomatic carapace as given at E of figure 47. The horseshoe-shaped acron (*Acr*) bearing the eyes encloses the region of the prosomatic somites (*I-VIII*), and sends posteriorly, between the lobes of the anteriorly curved cheliceral and pedipalp somites, a median tongue bearing the dorsal ocelli (*dO*). The structural conformity with the trilobite head (fig. 46 J) is exact, except for the greater number of somites included in the xiphosurid prosoma.

Students of the embryology of *Limulus* (Kishinouye, 1893, Iwanoff, 1933) have indicated the segmental divisions of the prosoma as subtending the lateral areas of the carapace bearing the compound eyes. Branches of the segmental nerves, the "haemal nerves" of Patten and Redenbaugh (1900), extend into these parts, but, as in the case of the trilobites, the location of the compound eyes on the lateral plates of the prosoma is sufficient proof that these plates belong to the eye segment, or acron. Hence, they cannot be lateral extensions of the median somites.

The gills of the trilobite legs, borne on coxal epipodites (fig. 48 D, *Eppd*), have not been retained on the prosomatic appendages of Xiphosurida, though an epipodite is present on the fourth leg (E, *Eppd*), but gill-bearing epipodites are highly developed on the opisthosomatic appendages, which are otherwise much reduced.

The prosomatic appendages of *Limulus*, except the chelicerac, as shown by Benham (1885), have the typical arthropod coxal musculature, consisting of dorsal promotor and remotor muscles (fig. 48 F, *I*, *J*), and ventral muscles (*K*, *L*). Of the latter, two (33, 34) are promotors and remotors, but two others (32m, 32n) are united proximally and evidently function as adductors. The dorsal muscles arise on the tergal carapace (C). The ventral muscles, however, are attached on an internal plate, or "entochondrite" (*k*), suspended in the ventral part of the body by dorsal muscles (*t-s*). The same structure (B) is characteristic of most of the Chelicerata, and a similar structure occurs in the gnathal segments of many of the Mandibulata (figs. 50 E, H, 51 B, *k*). Since the ventral muscles of the appendages should primarily arise on the ventral body wall, the "entochondrite" might be supposed to be a sternal derivative, but Schimkewitsch (1895, 1906) claims that in the Arachnida it is produced from transformed muscle tissue. In various mandibulate

arthropods some of the adductor fibers of the mandibles go continuously from one appendage to the other.

That the prosoma of *Limulus* contains at least a part of the eighth somite is evident from several structural features, but the writer's

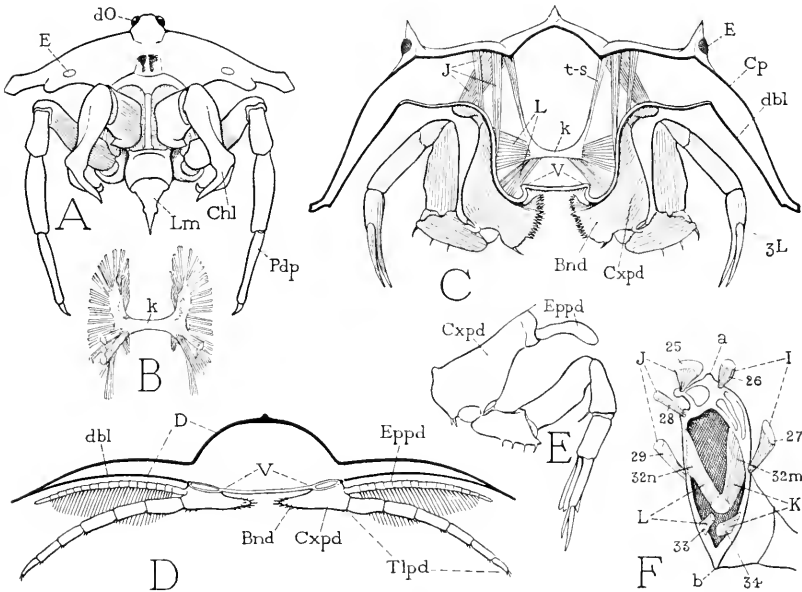


FIG. 48.—Structure of Chelicerata and Trilobita.

A, *Liobunum* sp. (Phalangida), anterior view of body, showing secondary preoral position of chelicerae above base of labrum. B, same, "endosternite" of prosoma with adductor leg muscles (suspensory dorsal muscle not shown). C, *Limulus polyphemus* Linn. (Xiphosurida), section of prosoma behind third legs, leg muscles somewhat diagrammatic. D, diagrammatic cross-section of a trilobite. E, *Limulus polyphemus*, fourth leg, with coxal epipodite. F, same, base of a left leg, mesal view, with muscle insertions (from Benham, 1885).

a, dorsal articulation of coxopodite; b, ventral end of coxal axis; Bnd, basendite; Chl, chelicera; Cp, carapace; Cxpd, coxopodite; D, dorsum; dbl, doublure; dO, dorsal ocellus; E, lateral eye; Eppd, epipodite; L, tergal promotor muscles of coxopodite; J, tergal remotor muscles of coxopodite; K, anterior ventral muscles of coxopodite; k, ligamentous "endosternite" on which ventral leg muscles are attached; L, posterior ventral muscles of coxopodite; 3L, third leg; Lm, labrum; Pdp, pedipalp; Tlpd, telopodite; t-s, tergal suspensory muscle of "endosternite"; V, venter; 26, 27, dorsal promotor muscles of coxopodite arising on carapace; 25, 28, 29, dorsal remotor muscles arising on carapace; 32m, 32n, anterior and posterior branches of coxal adductor arising on "endosternite"; 33, 34, ventral remotor and promotor muscles arising on "endosternite".

former statement (1936) that the prosoma and opisthosoma of *Limulus* are separated between segments VIII and IX is not strictly correct. The attachment of the muscles and the distribution of the nerves in this region demonstrate that the dorsal hinge between the prosomatic carapace and the opisthosomatic carapace lies within the

eighth segment itself, and not behind it, a narrow anterior median part of this segment being incorporated into the posterior margin of the prosoma, while lateral parts of it form the anterior lateral lobes of the opisthosomatic carapace (fig. 47 D, *VIII*). Six following segments of the opisthosoma are marked by the six pairs of impressions bordering the median elevation of the carapace, and by the six pairs of marginal spines. The intrasegmental division of the body into movable parts is not an anomalous condition; it occurs between the thorax and the abdomen of many insects, and is a necessary mechanical adaptation resulting from the primarily intersegmental attachments of the longitudinal muscles.

The six pairs of dorsal impressions on the opisthosoma of *Limulus* (fig. 47 D) and a pair of similar impressions on the posterior margin of the prosomatic carapace (*p*) form internally (*B*) a double series of tergal apodemes, the "entapophyses" of Benham (1885), of which the larger first pair (*VIIIAp*) is on the prosoma, and the other six pairs (*IXAp-XIVAp*) are on the opisthosoma. The tergo-sternal muscles of the five gill-bearing segments are shown by Benham to have their dorsal attachments (*12b-12f*) at the bases of the first five opisthosomatic apodemes, while the corresponding muscles of the opercular segment (*VIII*) arise at the bases of the corresponding prosomatic apodemes (*12a*). On the other hand, while the "external branchial muscles" of the gill segments have their dorsal attachments (*20b-20f*) just laterad of the first five opisthosomatic apodemes, the corresponding muscles of the operculum take their origins also on the opisthosomatic shield, but more laterally on the anterior lateral lobes. The muscle attachments, therefore, show that the dorsal part of the eighth segment has been divided between the prosoma and the opisthosoma, or, as Benham says, the first pair of tergal apophyses has been transferred from the opisthosoma to the prosoma. The dorsal longitudinal muscles between the prosoma and the opisthosoma of *Limulus* have been condensed into a single large bundle of fibers, the "arthrotergal muscle" of Benham, and the attachments of this muscle (fig. 47 B, 78) have extended somewhat anteriorly and posteriorly on the two body regions to acquire greater efficiency as a flexor of the opisthosoma.

The innervation of the hinge region of the carapace gives the same evidence of division within the eighth segment as that furnished by the musculature. As shown by Patten and Redenbaugh (1900), the nerves of the genital operculum proceed from the composite ventral ganglion of the prosoma, while the corresponding somatic nerves ("haemal nerves" of segment *VIII*) are distributed to the anterior

lateral lobes of the opisthosoma. From a comparative study of the position of the cardio-aortic valve in the Chelicerata, Petrunkewitch (1922) found that the valve is always between segments *VIII* and *IX*, and he therefore claimed that segment *VIII* is included in the prosoma of *Limulus*. His contention is but little affected by the modified view here shown to be in better accord with the facts. The operculum is anatomically more closely connected with the prosoma, from which it derives its innervation, than with the opisthosoma, and the partition of the tergum of its segment between the prosoma and the opisthosoma, as above noted, is but a necessary adaptation to give intersegmental action to primarily intrasegmental muscles.

The Eurypterida and Arachnida differ from the Xiphosurida in that the prosoma includes only six somites, and in this respect they are nearer to the Trilobita, which have only four prosomatic somites. The eurypterids and arachnids, however, lack the lateral expansions of the prosomatic carapace characteristic of the trilobites and xiphosurids, and, judging from the more anterior position of the lateral eyes (fig. 49 E, *E*), it seems probable that the acronal element of the prosoma is less extensive on the marginal areas of the latter, though medially it must include the region of the dorsal eyes (*dO*).

In a typical arachnid embryo (fig. 49 A) the somites are regular transverse sections of the trunk behind the large prostomial acron (*Acr*), which is produced laterally into a pair of cephalic lobes. Ordinarily there are no appendages on the acron, but Jaworowski (1891) has described a pair of apparent antennal rudiments in a species of *Trochosa* (C, *b*), and Pokrowsky (1899) found two pairs of transient precheliceral lobes in an embryo of *Pholcus opilionides* (B, *a, b*), the second of which, he says, correspond in position with the "antennal" rudiments described by Jaworowski. The nature of these embryonic lobes may be doubtful, but since the trilobites have well-developed antennae, there is no reason why embryonic vestiges of acronal appendages might not recur in some chelicerate forms. In adult Solpugida there is a pair of small appendages (fig. 49 F, *Ant?*) arising at the sides of the epistomal lobe, which are movable by muscles (G, *mcl*), and are, therefore, suggestive of being antennal remnants.

The cheliceral somite of the arachnid embryo (fig. 49 A, *I*) lies transversely immediately behind the acronal lobes; but in the adult this somite curves forward around the sides of the labrum from behind the mouth as in *Limulus*, so that the chelicerae come to have a preoral position above the labrum (fig. 48 A, *Chl*), though usually they are separated by a median epistomal bar extending downward

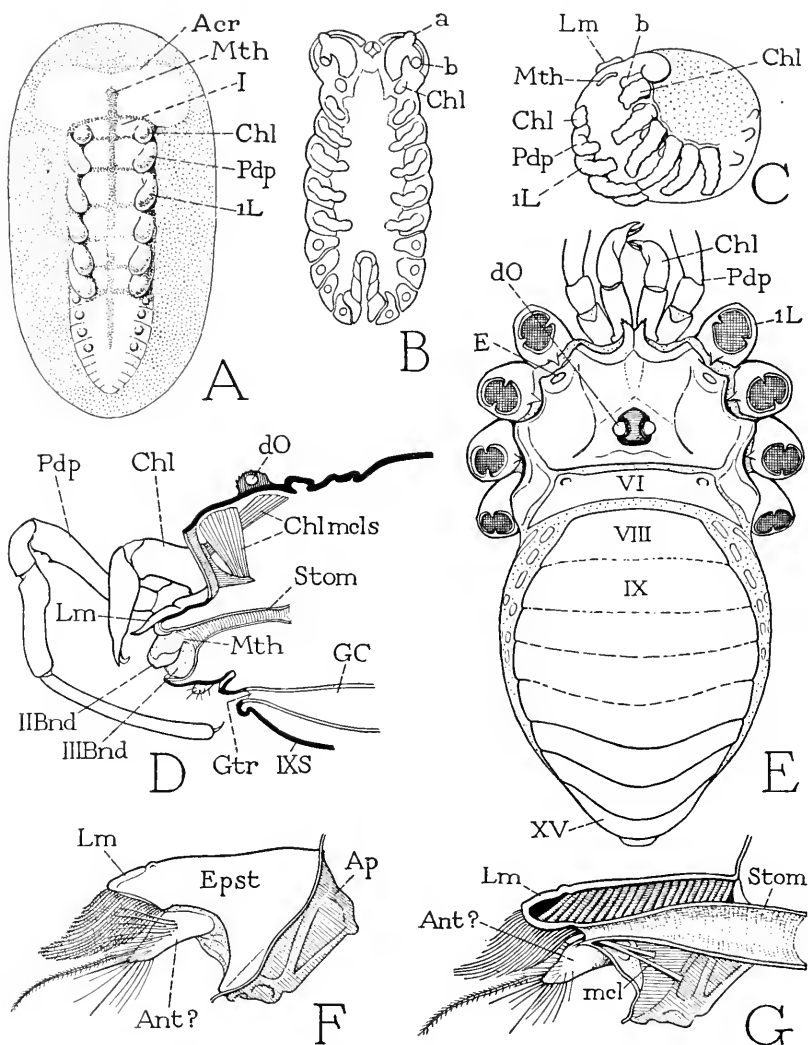


FIG. 49.—Embryonic and adult structures of Arachnida.

A, embryo of *Agelena labyrinthica* (from Balfour, 1880). B, embryo of *Pholcus opilionides* Schrank with two lateral lobes (*a*, *b*) on acron (from Pokrowsky, 1899). C, embryo of *Trochosa singoriensis* Laxm., with possible antennal rudiments (from Jaworowski, 1891). D, longitudinal section through anterior end of prosoma of a phalangid (*Liobunum*), showing anterior tergal attachments of cheliceral muscles. E, dorsal surface of phalangid (*Liobunum*), legs removed from coxopodites. F, epistomal lobe and labrum of a solpugid, lateral view, showing movable appendage (*Ant?*) at side of epistoma. G, same, longitudinal section, showing muscles of epistomal appendage.

a, possible preantennal rudiment of embryo; *Acr*, acron (cephalic lobe of embryo); *Ant?*, adoral (possibly antennal) appendage of adult solpugid; *b*, possible antennal rudiment of embryo; *Ap*, apodeme; *Chl*, chelicera; *Chlmcls*, cheliceral muscles; *dO*, dorsal ocellus; *E*, lateral eye; *Epst*, epistoma; *GC*, genital chamber; *Gtr*, gonotreme; *II Bnd*, *III Bnd*, basendites of second and third appendages; *IXS*, sternum of ninth somite; *1L*, first leg; *Lm*, labrum; *mcl*, muscles; *Mth*, mouth; *Pdp*, pedipalp; *Stom*, stomodaeum; *I-XV*, postoral somites.

to the labrum from the frontal region of the carapace. As in *Limulus* again, the chelicerae have only dorsal muscles, which arise on the anterior part of the carapace (fig. 49 D, *Chlmcls*).

The ancestors of the modern Mandibulata were represented in the more generalized members of the Protarthropoda that persisted after the trilobite-chelicerate branch had been given off from the main stem (fig. 54). The Protomandibulata undoubtedly retained the primitive centipedelike form of the protarthropods, but, as shown in the embryology of modern Mandibulata, the head at this stage must have been a composite protocephalon (fig. 39 C, *Prtc*) formed by an intimate union of the first somite (*I*) with the highly developed prostomial acron (*Acr*). It carried, therefore, the eyes (*E*), the labrum (*Lm*), the acronal appendages, or first antennae (*1Ant*), and the appendages of the included somite, which became a second pair of antennal organs (*2Ant*). The distinctive feature of the early mandibulates, however, was the presence of a pair of jaws, the mandibles (*Md*), developed from the bases of the appendages of the first postcephalic somite. Probably also the appendages of the following two somites were reduced in size and modified in a manner suggestive of their future transformation into maxillae; and perhaps a pair of paragnathal lobes was developed between the mandibles and the first maxillary appendages, since these structures are not present in the chelicerate branch.

The Crustacea represent the first offshoot from the mandibulate section of the arthropod stem that has given rise to a specialized group of modern forms (fig. 54). The wide recurrence among the Crustacea of cursorial appendages identical in segmentation with the legs of the trilobites can leave little doubt that the primitive crustaceans were polypodous walking animals, living on the bottom of the water or on aquatic plants along the ocean shores, and adapted to life in the water, as were the trilobites, by the development of branchial organs on exite lobes of the coxopodites. According to this view, the natatory appendages of swimming or purely pelagic Crustacea are legs that have been modified secondarily for swimming purposes, just as the gnathal appendages have been modified for feeding. It is a sound principle of ecology that pelagic forms in all cases have been derived from benthonic forms (see Hesse, Allée, and Schmidt, 1937, p. 179), and the fact that many of the more generalized modern Crustacea are pelagic is no argument that such forms are ancestral. The frequent biramous structure of crustacean appendages is entirely a crustacean feature, since the exopodite is a specially developed outer branch of the basipodite, and therefore has no counterpart in the Trilobita or in any other arthropod group.

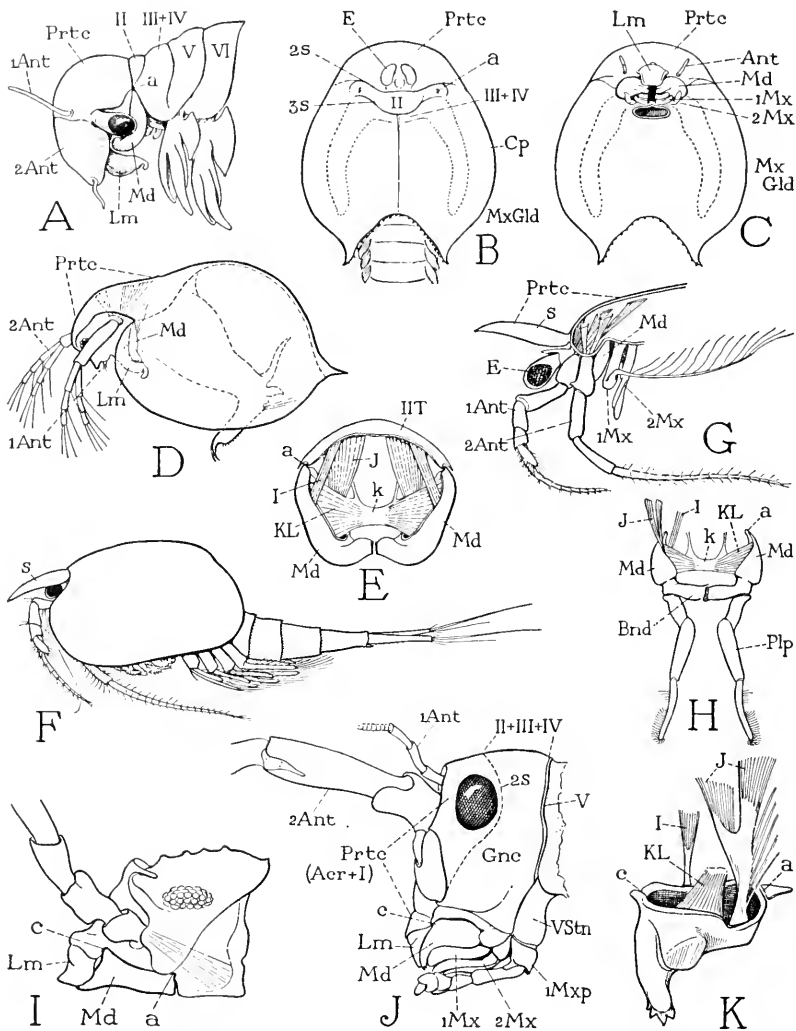


FIG. 50.—Cephalic structures of Crustacea in which the protocephalon (acron and first somite) is either the definitive head, or is united with several following somites to form a more extensive syncephalon.

A, *Eubranchipus vernalis* Hay (Anostraca): protocephalon a distinct head lobe (*Prtc*) separate from mandibular somite (*II*); maxillary somites (*III*, *IV*) united with each other. B, *Apus longicaudatus* Le Conte (Notostraca), dorsal view: mandibular and maxillary somites united with protocephalon, maxillary tergum produced in large cephalic carapace (*Cp*). C, same, ventral view of head, showing labrum, antennules, mandibles, and maxillae. D, *Daphnia pulex* Degeer (Cladocera): head structure as in *Apus*, body covered by bivalved maxillary carapace. E, *Eubranchipus vernalis*, detached mandibular segment, anterior view, showing mandibles suspended from tergum, and mandibular musculature. F, *Nebalia bipes* Fabr. (Leptostraca): bivalved carapace has same composition as in *Apus* and *Daphnia*. G, section of head of *Nebalia* showing muscle attachments of protocephalic appendages. H, mandibles of *Nebalia*,

The crustacean head is variable in structure according to the number of somites it contains. The most primitive crustacean head, as already noted, is a simple protocephalon formed by the union of the tritocerebral somite with the prostomial acron. A head of this type occurs in some of the Branchiopoda, and in all the Malacostraca except Leptostraca, Amphipoda, and Isopoda.

The best example of a protocephalic head is seen in the anostracan branchiopods. The head of *Eubranchipus*, for example (fig. 50 A, *Prtc*), is a large cephalic capsule bearing only the eyes, both pairs of antennae, and the labrum. Behind it is the small but distinct tergum of the mandibular somite (*II*), which supports the large mandibles (*Md*). The next following segment is evidently the two maxillary somites united (*III+IV*), since it carries the vestigial first and second maxillae. The muscles of the head appendages, including those of the eye stalks, the antennules, the second antennae (in the male), and the labrum, all take their origins on the walls of the head capsule. The mandibular muscles, on the other hand, arise on the mandibular tergum (*E*), except the adductors (*KL*), which are united on a median ligament (*k*) and thus form a zygomatic muscle between the two jaws.

The head of most of the other Entomostraca and of Leptostraca is a more extensive structure than that of the Anostraca, since it includes the mandibular and maxillary somites united with the protocephalon. The maxillary region of the head is often expanded to form a large cephalic shield, or bivalved shell, covering the anterior part of the body. In *Apus* (fig. 50 B) the region of the protocephalon (*Prtc*) forms a distinct anterior part of the definitive head bearing the eyes dorsally and the antennae and labrum ventrally (*C*). Behind the protocephalon the limits of the mandibular tergum (*B*, *II*) are clearly marked, but the maxillary terga (*III+IV*) are confluent as in

posterior view. I, *Porcellio* sp. (Isopoda), head, composed of protocephalon and four following somites (maxillae and maxillipeds removed). J, *Orchestoidea californica* Brandt (Amphipoda), head, same composition as in *Porcellio*, approximate division between protocephalic and gnathal regions indicated by broken line (*zs*). K, *Talorchestia longicornis* Say (Amphipoda), right mandible, mesal view.

a, primary (dorsal) articulation of mandible; *1Ant*, first antenna (antennule); *2Ant*, second antenna; *Bnd*, basendite; *c*, secondary (anterior) articulation of mandible; *Cp*, carapace; *E*, compound eye; *I*, tergal promotor muscles of mandible; *II-VI*, second to sixth somites; *ITT*, mandibular tergum; *J*, tergal remotor of mandible; *k*, ligament uniting ventral adductors of mandibles; *KL*, ventral adductor muscles of mandible; *Lm*, labrum; *Md*, mandible; *1Mx*, *2Mx*, first and second maxillae; *MxGld*, maxillary gland; *1Mxp*, first maxilliped; *Plp*, palpus; *Prtc*, protocephalon (acron+somite *I*); *zs*, suture between protocephalon and mandibular somite (*B*), or theoretical line of division between protocephalic and gnathal regions of head (*J*); *3s*, suture between mandibular and maxillary somites; *VStn*, sternum of first maxilliped somite.

Eubbranchipus (A). In the Cladocera (D) the general head structure and composition is the same as in *Apus*, except for the lateral compression of the maxillary shield, which gives the latter its "bivalved" form, but the intersegmental lines are lost, and the limits of the protocephalon (*Prtc*) are marked only by the attachments of the antennal muscles. The Leptostraca (F) have the cladoceran type of head and bivalved maxillary shield, but are distinguished by the presence of a large frontal lobe (*s*) projecting above the bases of the eye stalks. Here again the protocephalic area of the composite head is marked only by the origins of the muscles of the protocephalic appendages (G), including those of the eye stalks and the two pairs of antennae. The mandibles of the Leptostraca (*Nebalia*) retain the palpi (H, *Plp*), but their basal structure and musculature is the same as those of *Eubbranchipus* (E) and other Entomostraca.

The Malacostraca, other than Amphipoda and Isopoda, are commonly said to have a "cephalothorax," which includes the gnathal somites and a number of following somites up to a maximum of 12 in all. Most of this composite structure, however, which in its fullest development is covered by the carapace (fig. 51 C, *Cp*), is more truly a *gnathothorax*, since the true head is always a distinct though small protocephalic lobe more or less concealed beneath the overhanging rostrum (*r*) of the mandibular somite. When the protocephalon is detached, as shown in the figure (C), it is seen to be a distinct cephalic structure bearing the stalked eyes, both pairs of antennae, and the labrum. The typical malacostracan head is thus identical with the protocephalic head of the Anostraca (fig. 50 A, *Prtc*). Even in the Brachyura (fig. 51 D, E) the protocephalon is readily identified as such, though dorsally (D) it is much reduced, and is concealed in a pocket beneath the anterior margin of the carapace; ventrally (E) it carries a large epistomal plate and a small labrum. In the Stomatopoda, on the other hand, the protocephalon is highly developed (fig. 51 F, G), and its integumental sclerotization is broken up into several distinct plates (*d*, *e*, *f*, *g*), which, however, can in no sense be regarded as representing a "segmentation" of the head. The mandibles of the more generalized type found in the Malacostraca (B) are identical in their structure and musculature with the mandibles of Entomostraca (fig. 50 E, H).

The Amphipoda and the Isopoda (including Apseudidae), with regard to the structure of the head, do not appear to be properly classed with the rest of the Malacostraca, since the head (fig. 50 I, J) is an intimate combination of the gnathal somites (*II+III+IV*) with the protocephalon (*Prtc*), and thus resembles in its composition

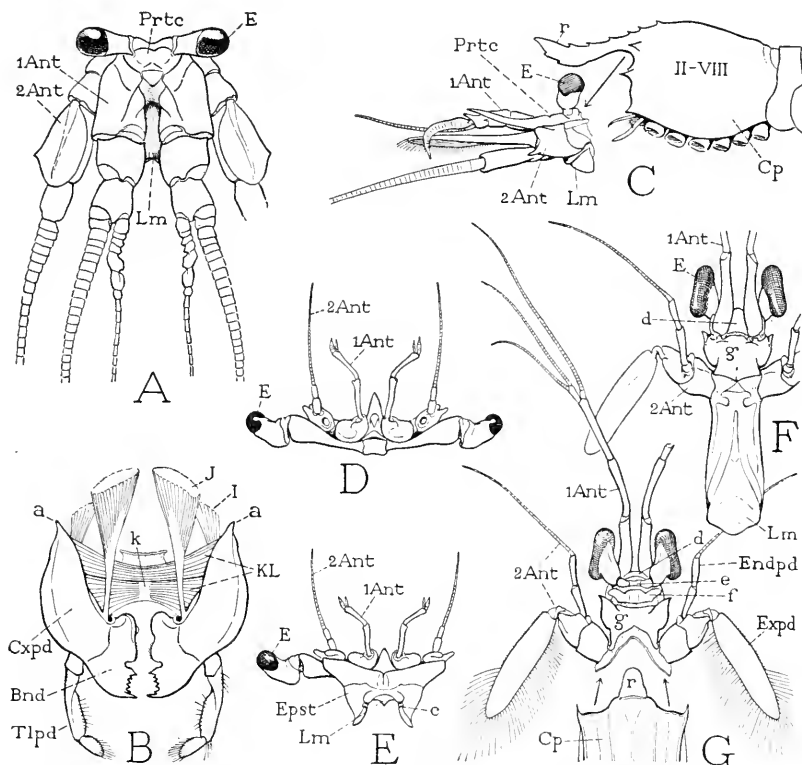


FIG. 51.—Cephalic structures of malacostracan Crustacea in which the definitive head is the protocephalon, as in Anostraca (fig. 50 A).

A, *Antaspides tasmaniae* Thomson (Syncarida), protocephalon and appendages, anterior view. B, same, mandibles and muscles, posterior view. C, *Spirontocaris polaris* (Decapoda-Macrura), showing protocephalon (Prtc) detached from carapace. D, *Callinectes sapidus* Rathbun (Decapoda-Brachyura) protocephalon and appendages, dorsal view. E, same, protocephalon, anterior view. F, *Chloridella panamensis* Bigelow (Stomatopoda), protocephalon and appendages, ventral view. G, same, protocephalon detached from carapace (Cp), dorsal view.

a, primary (dorsal) articulation of mandible; 1Ant, first antenna (antennule); 2Ant, second antenna; Bnd, basendite; c, secondary (anterior) articulation of mandible; Cp, carapace; Cxpd, coxopodite; d, anterior (ocular) division of protocephalon; E, compound eye; e, ocular plate of protocephalon; Epst, epistoma; Expd, exopodite; f, postocular dorsal plate of protocephalon; g, posterior (antennular) division of protocephalon; I, J, dorsal promotor and re-motor muscles of mandibles; II-VIII, second to eighth somites; k, adductor ligament of mandibles; KL, adductor muscles of mandibles; Lm, labrum; Prtc, protocephalon; r, rostrum of mandibular somite; Tlpad, telopodite (palpus).

the head of *Nebalia* and of such entomostracan forms as *Apus*, *Daphnia*, and others, though in form it often has a striking resemblance to the head of a hexapod mandibulate. However, in both the amphipods and the isopods the head usually includes also the first maxilliped somite and its appendages (fig. 50 J, *1Mxp*), and may in addition bear the second maxillipeds. The mandible acquires a secondary anterior articulation with the cranium (I, J, K, *c*), by which its action is limited to a hinge movement on a horizontal axis between its two articular points (K, *a*, *c*). The same mandibular mechanism has been independently developed in the decapod Crustacea and in the pterygote Hexapoda. While the head structure of the Amphipoda and Isopoda sets these groups apart from other Malacostraca, it does not necessarily relate them to any other group.

The final type of head developed in the Arthropoda is that characteristic of the myriapods and hexapods, and must have evolved in the common ancestors of these groups represented in the post-crustacean, protomyriapodan section of the main arthropod stem (fig. 54). The head of all the myriapod and hexapod groups is a highly standardized structure, composed of the protocephalon and the three gnathal somites, so closely united that little evidence of the original segmentation remains, except in the presence of the appendages (fig. 53 A), and even here the evidence is obscured by the loss of the second antennae. In early ontogenetic stages, however, the gnathal somites are entirely distinct from a large anterior cephalic lobe that usually includes the second antennal somite, which may bear vestiges of its former appendages. The Protomyriapoda must have had compound eyes, since eyes of the compound type recur finally in the Hexapoda; they likewise must have carried paragnathal lobes of the head from the Crustacea to the Hexapoda, though these organs have disappeared in the modern myriapodous forms. The maxillary appendages probably were no more specialized in the protomyriapods than in modern Chilopoda (fig. 53 A, C). The mandibles lost the telopodites, but they developed a special feature of which no suggestion is to be found in the Crustacea, namely, a mobile gnathal lobe, the lacinia, movable by muscles arising in the mandibular base and on the walls of the cranium. The mandibular lacinia is retained as a movable lobe in modern Symphyla (fig. 52 E, *Lc*) and Diplopoda; in the Chilopoda it is not separated from the stipital region of the mandible (fig. 53 E, F), though it is provided with strong stipital and cranial muscles (F, *I3*, *10*); in the Pauropoda and Hexapoda (fig. 52 F) apparently it has united with the stipes (*St*), producing a solid jaw of the crustacean type, and its muscles have disappeared.

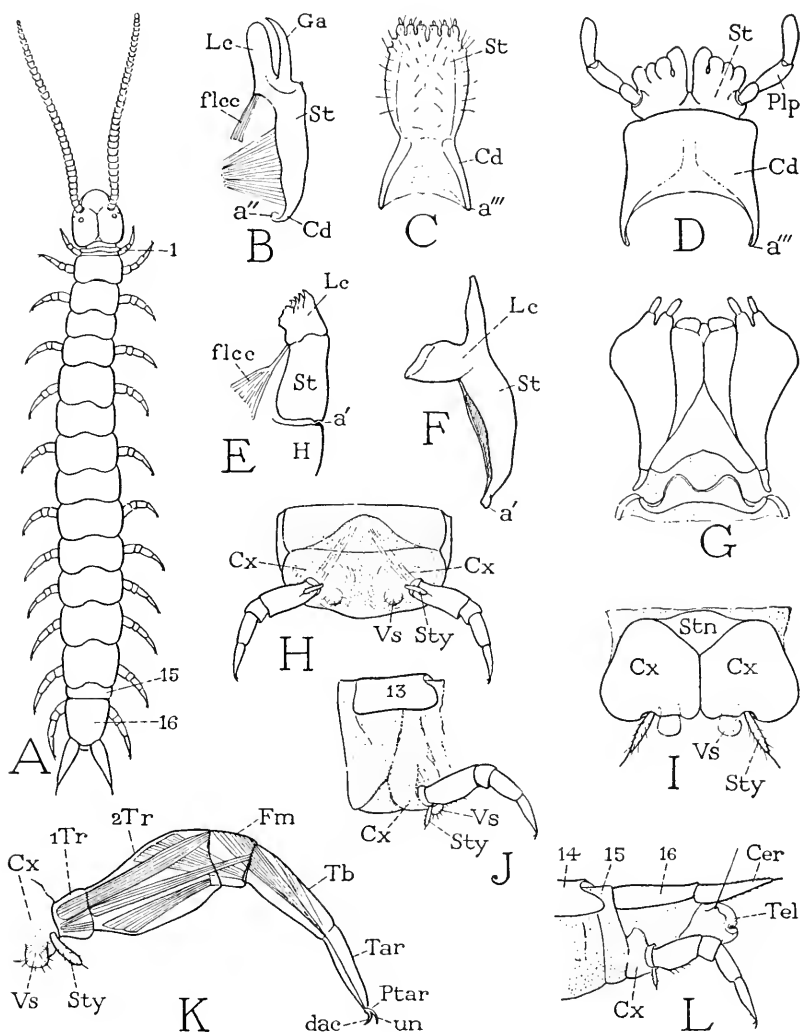


FIG. 52.—Symphyla, Diplopoda, and Thysanura.

A, *Scutigrella immaculata* Newport (Symphyla). B, same, maxilla. C, same, labium. D, labium of *Machilis* sp. (Thysanura). E, mandible of *Scutigrella*. F, mandible of *Machilis*. G, gnathochilarium of *Pontaria virginiana* (Drury) (Diplopoda). H, thirteenth body segment of *Scutigrella*, ventral view. I, seventh abdominal segment of *Machilis*, ventral view. J, thirteenth body segment of *Scutigrella*, lateral view. K, last leg of *Scutigrella*, posterior view. L, terminal segments of *Scutigrella*, lateral view.

a, *a'*, *a'''*, cranial articulations of mandible, maxilla, and labium; *Cd*, cardo; *Cer*, cercus; *Cx*, coxa; *dac*, dactyl (clawlike remnant of dactylopodite); *flec*, cranial flexor muscle of lacinia; *Fm*, femur; *Ga*, galea; *H*, head; *Lc*, lacinia; *Plp*, palpus; *Ptar*, pretarsus; *St*, stipes; *Stn*, sternum; *Sty*, stylus; *Tar*, tarsus; *Tb*, tibia; *Tel*, telson; *1Tr*, first trochanter; *2Tr*, second trochanter (prefemur); *un*, lateral claw (unguis) of pretarsus; *Vs*, eversible vesicle; *1-16*, body segments.

The maxillary appendages in Symphyla and Hexapoda have acquired two endite lobes of the stipes (lacinia and galea), but the palpi have been lost in Symphyla (B).

The last important event in the evolution of arthropod head appendages was the union of the bases of the second maxillae to form a single median organ, the so-called labium. The labium took its origin in the common ancestors of the Symphyla, Diplopoda, Pauropoda, and Hexapoda, which constituted the third and most prolific branch of the arthropod stock (fig. 54). The primitive structure of the labium is best preserved in the more generalized hexapods (fig. 52 D); in the Symphyla (C), Pauropoda, and Diplopoda (G) it has lost the telopodites, or palpi, and in the diplopods it forms at least a part of the complex gnathochilarium (G).

Crampton's (1928) phylogenetic conclusions drawn from comparative studies of the arthropod head differ radically in some respects from the concept of arthropod relationships here deduced from the same source. Crampton believes that the first arthropods derived from annelid precursors were probably prototrilobites, and that from the latter were evolved in one direction the Trilobita and Chelicerata, in another the Protocrustacea, which last in turn produced the higher Crustacea, while finally, from the malacostracan Crustacea were evolved the Myriapoda and Hexapoda.

To the writer it would seem that if the Protarthropoda are conceded to have been derived from wormlike ancestors, whether annelidan or protonychophoran, by a sclerotization of the integument and a jointing of the appendages, they must have taken on at once a centipedelike form. According to the theory here proposed, therefore, a long, unbroken line of slender polypodous arthropods has persisted from the ancient protonychophoran progenitors to the modern chilopods. Along this line have been carried the features common to all the arthropods, while new characters evolved in the main line itself have been distributed to subsequent lateral branches, where in some cases they have persisted in their original state, in others they have still further evolved, and in still others they have been lost.

The first lateral branch from the arthropod stem was that of the Prototrilobita (fig. 54), which produced the Trilobita and the Chelicerata. In this branch cephalization united the first four somites with the acron to form the trilobite "head," and continued in the Chelicerata until the "prosoma" contained six and eight somites. Meanwhile, in the main protarthropod stem, cephalization produced a more simple head (protocephalon) consisting of the acron and only the first somite, but the appendages of the second somite were converted into a pair

of jaws. The protarthropods thus developed into Protomandibulata. At this point arose the crustacean branch, in which the simple protocephalon is still the definitive head in a large number of forms, though

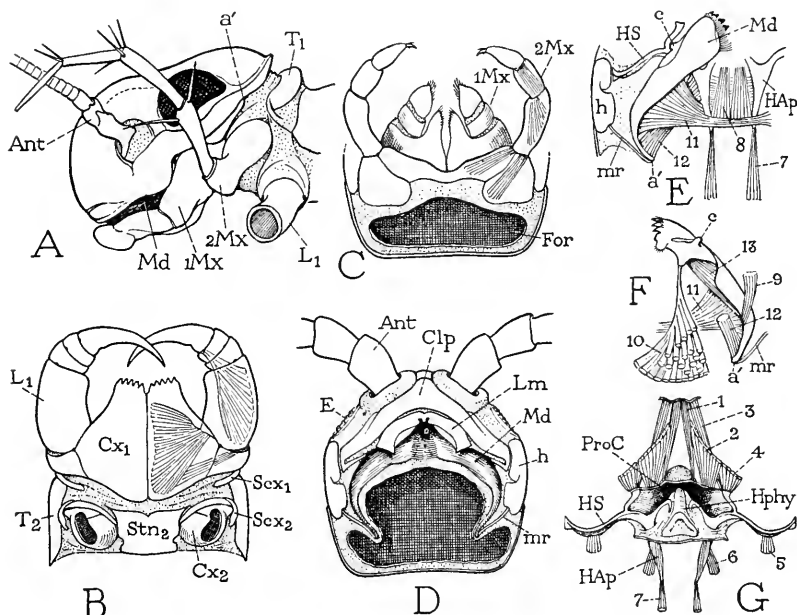


FIG. 53.—Head and mouth parts of Chilopoda.

A, head of *Scutigera forceps* Raf. B, poison claws (first legs) and second body segment of *Lithobius* sp., ventral view. C, first and second maxillae of *Lithobius*, ventral view. D, head of *Lithobius* with maxillae removed, ventral view. E, right mandible and associated head structures of *Lithobius*, ventral view. F, right mandible of *Lithobius*, dorsal view. G, hypopharynx, hypopharyngeal suspensoria, and preoral mouth cavity of *Lithobius*, ventral view (labrum and clypeus removed).

a', primary posterior articulation of mandible; *Ant*, antenna; *c*, secondary anterior articulation of mandible; *Clp*, clypeus; *Cx*, coxa; *E*, eye; *For*, foramen magnum; *h*, ventral inflection of cranium; *HAp*, hypopharyngeal apodeme; *Hphy*, hypopharynx (metastoma); *HS*, hypopharyngeal suspensorium (fulcrum); *L*, leg; *Lm*, labrum; *Md*, mandible; *mr*, mandibular rod; *1Mx*, *2Mx*, first and second maxillae; *ProC*, preoral mouth cavity; *Scx*, subcoxa; *Stn*, sternum; *T*, tergum; *1*, *2*, frontal and clypeal muscles of labrum; *3*, *4*, frontal and clypeal muscles of hypopharyngeal suspensorium; *5*, *6*, *7*, cranial muscles of same; *8*, ventral dilator muscles of pharynx; *9*, cranial muscle of mandibular stipes; *10*, cranial flexor of mandibular lacinia (origin lateral on cranium); *11*, adductor muscle of mandible; *12*, protractor muscle of mandible; *13*, stipital flexor of mandibular lacinia.

in several groups a more extensive head has been evolved by adding to the protocephalon the following three, four, or five somites. Cephalization, however, continued also in the main protomandibulate line, and produced here a composite head of standardized structure in

which the three gnathal somites were intimately combined with the protocephalon, while the appendages of the protocephalic somite (second antennae) were suppressed. The Protomandibulata now became Protomyriapoda. A composite head has thus been produced along three separate lines of arthropod evolution, but in each case with characteristic differences.

The Protomyriapoda had all the characters common to the several groups of arthropods finally derived from them, and also older characters earlier transmitted to the Crustacea, which later appear in one or more descendent groups, and are lost in others. From the protomyriapods there arose the final persistent arthropod branch, the Protosymphyla, while the main stem continued into the relatively generalized modern Chilopoda (fig. 54). The Protosymphyla developed a labium by the union of the bases of the second maxillary appendages, and so characteristic is this feature of all their descendants, including the modern Symphyla, Diplopoda, Pauropoda, and Hexapoda, that this group as a whole might be distinguished as the *Arthropoda labiata*. The chilopods have developed few special features other than the conversion of the first legs into a pair of poison claws, but they have lost certain features of the protomyriapods.

COELOMIC ORGANS OF ADULT ARTHROPODS

In no modern adult arthropod is there retained a complete series of coelomic sacs, but remnants of the coelom are preserved as the lumina of the gonads and genital ducts, of various glands having an excretory or accessory genital function, and perhaps of other glandular structures. The embryonic development of the coelomic sacs of the Onychophora very probably recapitulates fairly closely the phylogenetic history of the coelomic sacs in both the Onychophora and the Arthropoda. The primitive coelom of these animals undoubtedly consisted of a full series of paired segmental cavities, each opening to the exterior through a ventral diverticulum of the coelomic wall connected with the ectoderm mesad of the base of the corresponding appendage. The cavities must have served for the accumulation of excretory products, and for the retention of the developing germ cells, and the outlets gave vent to both the excreta and the gametes (fig. 34 A). The more primitive annelids do not have permanent coelomic openings, and it seems doubtful that the simple coelomoducts of the Onychophora had a common origin with the metanephridia of the higher Annelida, since the metanephridia are outgrowths of the posterior walls of the coelomic sacs and each opens through the segment following.

Early in the evolution of the common ancestors of the Onychophora and Arthropoda, judging from the embryonic development of modern Onychophora, the coelomic cavities were differentiated into dorsal compartments (fig. 34 B, *a*) containing the proliferation centers of the germ cells in their walls, and into ventral compartments (*b*) opening through the coelomoducts (*c*, *d*). With the complete separation of the two series of compartments (C), the dorsal compartments became gonadial sacs (*G*) and the ventral compartments (*b*) became nephridial sacs. The gonadial sacs, being deprived of outlets, united with one another on each side and formed a pair of longitudinal gonadial tubes (E, *G*), which retained exit passages through one pair of coelomic sacs that maintained their integrity and served as genital ducts. The ventral sacs and their respective coelomoducts were transformed into specific segmental excretory organs, or nephridia. It is thus clear that the genital ducts are not "modified nephridia," as they are often said to be, but that the genital ducts and the nephridia are separate products of the primitive open coelomic sacs, and hence, when once individually established, cannot be interchangeable in function. However, because of the variable position of the genital ducts in the Arthropoda, it is evident that a different pair of coelomic sacs has been retained in different groups to serve as genital outlets.

Excretory organs of coelomic origin in the Arthropoda are represented by the coxal glands of Chelicerata and the nephridial head glands of Crustacea, and perhaps also by certain head glands of Diplopoda, Chilopoda, and apterygote Hexapoda. The coxal glands of the Chelicerata, with one exception, consist of a single pair of excretory organs situated in the prosoma and opening at the bases of the appendages. Each gland in its fullest development is a composite structure composed of several lobes or saccules derived from coelomic sacs and united upon a common tubular base, the so-called "stolon," or "labyrinth," composed of glandular cells and tubules, and is connected with the exterior by one or two segmental ducts. The organ is, therefore, variable in features that might be supposed to vary in a composite structure of such a nature, as in the number of coelomic sacs involved, the number of segmental openings, and the position of the openings. The excretory head glands of Crustacea include a pair of antennal glands ("green glands") and a pair of maxillary glands ("shell glands"). The first are present in the adult stage only in the Malacostraca; the second occur in the Entomostraca and in some Malacostraca; both pairs are present in *Nebalia* (Manton,

1934). The maxillary glands are usually simple tubes or sacs, but the antennal glands may take on a highly complex structure.

The coxal glands of *Limulus* are a pair of large brick-red organs lying in the sides of the prosoma. Each organ consists of four successive glandular lobes arising from a common longitudinal stolon composed of numerous connecting tubules, and of a long coiled duct that proceeds from an end-sac in the fourth lobe and opens behind the base of the fifth appendage (third leg). According to Patten and Hazen (1900) the nephridial lobes are developed from masses of mesodermal cells derived apparently from the somatic walls of the coelomic sacs of the second, third, fourth, and fifth somites. Similar masses of cells in the first and sixth somites degenerate and disappear. The duct arises as a tubular diverticulum of the fifth coelomic sac, which latter becomes the fourth nephridial lobe. A short terminal part of the definitive duct is formed as an ectodermal invagination at the external orifice of the mesodermal duct.

The coxal glands of Arachnida are best known from the work of Buxton (1913, 1917, see also Petrunkewitch, 1933, and Chickering, 1937). A relatively primitive condition is found in the araneid groups Liphistiomorphae and Mygalomorphae, in which each gland has two saccules, one in the third, the other in the fifth segment, both connected with a long convoluted tubular labyrinth, from which two outlet ducts proceed to the exterior, one opening behind the third appendage, the other behind the fifth. Such an organ would appear to be a composite structure formed by the union of three consecutive segmental glands. In certain genera of the Amblypygi group of the Pedipalpida the gland of the fifth segment is shown by Buxton (1917) to be an independent organ opening separately on the fifth segment. In the Uropygi each gland has two saccules but only a single opening, which is on the third segment. All other Arachnida have but a single saccule for each lateral gland and a single outlet, but the opening is at the base of the second appendage (pedipalp) in Solpugida and Palpigradida, at the base of the third appendage (first leg) in Araneida, excepting the two groups above mentioned, and at the base of the fifth appendage (third leg) in Scorpionida and Phalangida, as in *Limulus*. Buxton calls attention to the correspondence of the coxal glands of Solpugida and Palpigradida with the salivary glands of Onychophora, the organs in each case having their opening on the second postoral body somite.

Studies on the development of the arachnid coxal gland appear to leave no doubt that the organs are derivatives of coelomic sacs with coelomoducts formed as direct diverticula from the sacs as are the

coelomic ducts of Onychophora. Brauer (1895) has shown that in the embryonic development of the scorpion there are formed five pairs of diverticula from the coelomic sacs of somites *III*, *IV*, *V*, *VI*, and *VIII*, respectively, of which those of the fifth and eighth somites acquire openings to the exterior. The coelomic sacs and their diverticula in the fifth somite develop into the definitive coxal glands, the coelomic diverticula of the eighth somite become the genital ducts, and the sacs and diverticula of the other segments disappear. According to Kishinouye (1894) the development of the coxal glands in the araneid genera *Lycosa* and *Agelena* shows that each organ is a composite structure formed of small parts of the coelomic sacs of somites *III*, *IV*, and *V*, but only the first acquires an opening to the exterior.

The nephridial glands of the Crustacea, being individual organs, resemble the simple nephridia of the Onychophora rather than the composite coxal glands of the Chelicerata. Each organ consists of a mesodermal end-sac, a mesodermal canal, which may become highly complex in form, and a short exit duct of ectodermal origin (see Cannon and Manton, 1927, and Manton, 1930). The embryogeny of the crustacean excretory glands, however, is in some cases complicated by an indirect course of development.

The antennal gland of *Hemimysis lamornae* is said by Manton (1928) to be formed from two masses of cells derived from the antennal mesoderm, one of which produces the end-sac, the other the canal. The canal becomes attached distally to the ectoderm, and a small ingrowth from the latter forms a short ectodermal exit duct. Where the canal touches the wall of the sac, a compact group of 7 or 8 cells bulges into the lumen of the canal, and at this point the sac and the canal become united, but the only visible communication between them, Manton says, is by fine rather vague channels passing through the nephrostome cells. According to Vogt (1935) the antennal mesoderm of *Mysis relicta* produces only the canal and a sheet of connective tissue membrane in the base of the antenna, to which the canal becomes attached. A group of 8 cells in this membrane then forms the nephrostome. The true end-sac, Vogt claims, is constructed from adventitious connective tissue cells that wander into the antenna from the thoracic segments and form the end-sac beneath the nephrostome membrane. Vogt contends that the development of the antennal gland of *Mysis relicta* so closely resembles the development of an annelid nephridium that the two organs must be homologous structures, the nephrostome membrane of *Mysis* representing a dissepiment in the annelid. To the writer a parallelism in the two

cases is far from evident, and the development of the mysid antennal gland seems better explained as a secondary modification of the developmental processes that give rise to the coxal glands of Arachnida and the nephridia of Onychophora.

Most of the tracheate Mandibulata have a series of head glands pertaining to the gnathal somites, the openings of which lie mesad of the appendage bases, or are displaced anteriorly or posteriorly when the bases of the two appendages of a pair are united. Some of these glands have been shown to have an apparent excretory function, because of their property of eliminating from the blood particles of carmine injected into the body of the animal, and such glands also have a complex structure, usually described as consisting of a saccule, a labyrinth, and a duct. Hence, various writers have claimed that glands of this type represent nephridial organs corresponding with the excretory head glands of Crustacea, though little evidence as to their embryonic origin has been produced.

The gnathochilarial glands of the Diplopoda have been shown by Bruntz (1903) to collect injected carmine from the blood, and they are said by Heathcote (1886) to be derived from the mesoderm in embryonic development. Likewise, according to Bruntz (1908) and Philpitschenko (1928), a pair of labial glands of apterygote insects have an excretory function and a nephridialike structure. These glands open either separately (*Campodca*, *Japyx*) between the hypopharynx and the labium, or (*Machilis*, *Lepisma*) their ducts unite in a common median duct, and are joined by the ducts of a pair of "posterior salivary glands." The labial glands of the apterygote insects, particularly those of Thysanura, would so evidently seem to be the same as the labial glands of pterygote insects, which are commonly found to be ectodermal organs, that it is difficult to believe they are not homologous structures, regardless of their function. In the Chilopoda, according to Fahlander (1938), there are present generally three pairs of head glands associated with the bases of the gnathal appendages, but in addition there is another pair having a complex structure suggesting an excretory function. These glands have each two openings, one mesad of the base of the first maxilla, the other behind the base of the second maxilla. Fahlander contends, therefore, that each gland has been formed by the union of two nephridial organs pertaining to the maxillary somites. The morphological status of all such glands must yet be determined by a study of the embryonic development.

THE GENITAL DUCTS

The student of arthropod phylogeny is confronted at every turn with the vexing problem that arises from the different position of the genital outlets in the various arthropod groups, and in recent years much discussion has been given to the question as to how the heterogoneate condition came about (see Tillyard, 1930, 1932, 1935, Snodgrass, 1933, 1936, Reynolds, 1935, Imms, 1936). Two phases of the problem have been somewhat confused, namely, that pertaining to the position of the openings of primary lateral ducts, and that pertaining to the position of secondary median ducts. The opening of a median duct is subject to migration, usually in a posterior direction; the openings of lateral ducts are closely associated with particular segments, since the lateral ducts themselves represent specific pairs of segmental coelomic sacs.

The possible migration of lateral genital ducts is narrowly restricted because of the limitations imposed by the transverse segmental nerve trunks; a secondary median duct formed by invagination of the ventral wall of the body, however, lies beneath the ventral nerve cords, and may, therefore, become lengthened from one segment to another by an extension of its connection with the body wall. There is no evidence to support Tillyard's (1930) contention that segmental gonads were once connected by a common duct, which has retained a single definitive opening on different segments in different arthropods, because when the germaria were segmentally arranged they were contained in the dorsal parts of segmental coelomic sacs with individual openings to the exterior, and the serial union of the dorsal parts of the coelomic sacs has produced the definitive tubular gonads opening through a single pair of coelomic sacs, while the ventral parts of the other sacs discharging through the coelomoducts became nephridial sacs. Likewise, Tillyard's (1935) second proposal that a heterogoneate condition has arisen by a variation in the number of somites formed before or behind the primary genital somite cannot be accepted for the reason that somite formation in the genital region is primitively teloblastic.

Inasmuch as the primary lateral genital ducts represent specific coelomic sacs that have been retained to serve as genital outlets, a segmental difference in the position of the genital openings is to be explained only as the result of mutations that have been effective in the organizer of the zone of teloblastic growth, which determines what particular pair of coelomic sacs shall be utilized as genital exits. A branching of the embryonic lateral ducts has been observed by

Heymons and by Wheeler in Dermaptera, and, according to Heymons (1901), the definitive ducts of *Scolopendra* are formed from two united pairs of coelomic sacs. In such cases we have, perhaps, examples of the supplanting of one pair of exit sacs by another pair.

The heterogoneate condition of modern arthropods, therefore, must be the result of mutations that occurred among ancestral forms. The faculty of mutation affecting the position of the genital ducts was carried over into the entomostracan branch of the Crustacea, and was not entirely extinct in the early forms of the Hexapoda. Moreover, in the Chilopoda, as in the Onychophora, there still exists a variability as to the segment of the genital ducts, for, though the genital outlet is always on the subterminal segment in Chilopoda and on the antepenultimate segment in Onychophora, the genital segment is not morphologically the same somite in all cases, since the number of somites preceding it may be quite different in different genera. In the Geophilomorpha, furthermore, the number of pregenital somites is said to vary even among individuals of the same species.

VII. PHYLOGENETIC CONCLUSIONS

1.—A planulalike creature with an open posterior blastopore was probably the ancestor of the Metazoa. A creeping form adapted to feeding on a subsurface by the forward elongation of the blastopore on the under side of the body might readily have evolved into a worm by the partial closure of the blastopore, producing thus an alimentary canal with a ventral subapical mouth and a terminal anus. The subapical position of the mouth differentiated the animal into an acronal sensory region, or *prostomium*, and a postoral visceral and motor region, the body, or *soma* in a restricted sense.

2.—The unsegmented progenitors of the annelids were probably small, creeping, wormlike creatures having a simple alimentary canal, a mouth on the anterior part of the under surface of the body, and a terminal anus. Locomotion on solid surfaces was effected by a ventral clothing of cilia, and body movements were produced by a system of muscle fibers on the inner surface of the body wall, derived from the ectoderm. The body cavity was a blastocoelic haemocoele, and was largely occupied by lateral bands of a mesoblastic parenchyma proliferated in the gastrula stage from endodermal or ectodermal teloblastomeres. The nervous system consisted of longitudinal and circular nerve tracts centering in ganglionic cell groups of the prostomium, which latter eventually united to form a "brain." Sensory organs may have included tactile tentacles and photoreceptive "eye spots" located on the prostomium.

3.—The annelidan progenitors acquired a more effective body movement by the attachment of the longitudinal somatic muscle fibers at several successive rings on the body wall, and by the accompanying formation of transverse muscular septa at the resulting integumental grooves. The body region of the wormlike animal in this way became differentiated into a small number of consecutive motor units, the *primary somites*. To regulate the new muscular mechanism of metameric movement, there was developed from the body surface of contact with the substratum a new somatic nervous system in the form of ventral nerve cords with ganglia corresponding with the myotomes. The primary and secondary nervous systems were then unified by a connection of the ventral nerve cords with the brain, and the somatic elements of the primary system disappeared. The ingrowth of the septal muscles cut the parenchymatous mesoblast bands into segmental blocks, and the latter became excavated by cleavage spaces (primitive coelomic cavities) for the accumulation of body fluid containing waste products. Excretory organs, if present at this stage, were simple nephridial tubules extending from the ectoderm into the haemocoel, where they were associated with the mesoblast cavities. The inner parenchymal cells lining the cavities formed epithelial coelomic sacs, but the outer cells, being still an undifferentiated tissue, were converted into muscle fibers and connective tissue. The secondary muscles thus formed reinforced the primary somatic muscles already present, and eventually became the major part of the muscular system. The germ cells remained in a mass of undifferentiated tissue near the posterior end of the body, and the gametes were liberated probably through a pore or temporary rupture of the body wall. The primitive segmented worms evolved in this manner from unsegmented progenitors were the ancestors of the annelids.

4.—To increase the reproductive function, the subterminal genital region of the primitive oligomeric annelids was enlarged by the successive generation of new somites from its undifferentiated tissue. A series of secondary *teloblastic somites* duplicating the structure of the primary somites was thus interpolated between the primitive body of the worm and a small postgenital terminal cone containing the anus. The multiplying germ cells spread into the haemocoel of the new somites, and groups of them became lodged in the walls of the coelomic sacs. The ripening germ cells were now discharged into the coelomic cavities, which latter thus became gonadial as well as nephric in function. Since the coelomic sacs as yet probably had no permanent openings, the gametes must have been liberated through temporary pores of the body wall, through secondary genital openings

into the nephridia, or by the autotomous separation of the genital somites. At this stage the generalized annelids had acquired the fundamental characters common to the higher Annelida, the Onychophora, and the Arthropoda.

5.—The increase in the size of the body by the addition of the teloblastic genital somites created a demand for a still greater efficiency of locomotion, and, according to the nature of the response to this demand, two divergent groups of worms were evolved from the generalized annelids. The members of one group acquired segmental clusters of eversible and retractile chaetae serving as adjuncts to the somatic muscular system by maintaining a hold on surfaces of contact; the members of the other group developed segmental pairs of lobelike outgrowths of the body wall containing extensions of the somatic muscles, which served as primitive legs. The chaetae-bearing forms gave rise to the Chaetopoda; the lobopod forms were the ancestors of the walking Onychophora and Arthropoda.

6.—From the primitive chaetopods were evolved the several groups of modern annelids. By the extension of open tubes from the posterior walls of the coelomic cavities to the exterior, a more efficient type of excretory organ (metanephridium) was developed, which could serve also for the liberation of the gametes. The Polychaeta are distinguished particularly by the elaboration of external structures of various kinds, while the Oligochaeta and Hirudinea have achieved a higher development of internal organs and functions. The locomotor powers of the Polychaeta were increased by the development of lateral lobes of the body wall supporting the segmental groups of chaetae, and in most forms each lateral pair of chaetigerous lobes eventually combined to produce a single locomotor organ, the parapodium. The parapodia served for progression on solid surfaces, and became also effective adjuncts to the undulatory motion of the body during swimming.

7.—The lobopod annelids became further differentiated from their chaetopod relatives by a chitinization of the entire cuticula, and by the suppression of all the cephalic tentacles except one pair probably corresponding with the palpi of the Polychaeta. They also acquired outlets from the coelomic sacs to the exterior, but the exit ducts were formed as diverticula from the ventral walls of the sacs and opened each on the segment of its sac mesad of the base of the corresponding leg. The germ cells were located in the walls of the dorsal parts of the coelomic sacs, and the primitive coelomoducts discharged both excretory matter and the gametes. The coelomic sacs, however, soon became divided into dorsal gonadial compartments and ventral nephric

compartments. The gonadial sacs of each lateral series united with each other, forming thus a pair of tubular gonads, which opened to the exterior through one pair of undivided coelomic sacs and their outlet ducts. The ventral nephric sacs now became exclusively excretory reservoirs, and, with the coelomoducts, formed a series of nephridial organs along each side of the body. As a result of the conversion of the original coelomic sacs into gonadial sacs and nephridial sacs, the haemocoel was restored as the definitive body cavity.

At this stage of their evolution, the lobopod annelids assumed the status of *Protonychophora*. Some of the *protonychophorans* retained the flexible integument of the worms; others developed a sclerotization in the cuticula, and thus acquired an external skeleton of cuticular plates. The soft-skinned forms, preserving some of the general aspects of their annelidan ancestors, evolved into the modern *Onychophora*; the armored forms gave rise to the *Protarthropoda*. Since the members of both groups were well adapted by their leglike appendages to a walking mode of progression, many of their descendants found an advantageous habitat on land.

8.—The *Onychophora* retained the cylindrical wormlike form, but they lost the segmented structure in the integument and musculature. The lobiform appendages became more efficient locomotor organs through the development of an incipient segmentation, and the acquisition of terminal claws, but the first postoral appendages were converted into a pair of jaws. The single pair of prostomial tentacles took an apical position by migrating forward on the dorsal surface of the head, but their nerve tracts were united by a commissure in the posterior part of the brain. The eyes retained the annelid type of structure. The somatic nerve cords, which presumably must have been ganglionated in the segmented generalized annelids, became simplified by a redistribution of the neurocytes, and took widely separated positions along the sides of the body. The ganglia of the jaw somite, however, united with the cerebral ganglion of the prostomium and became posterior lobes of the brain. The coelomic sacs of the penultimate somite, regardless of the total number of somites in the body, were retained intact to serve as genital outlets; the persisting remnants of most of the other coelomic sacs became small end-vesicles of the coelomoducts, which formed nephridial excretory organs.

9.—The *Protarthropoda*, because of the hardening of the integumental cuticula, lost the flexibility and contractility of their annelidan ancestors and *onychophoran* relatives, and, to compensate, developed

a mechanism of telescopic movement between successive body segments by the simple device of retaining nonsclerotized areas in the posterior parts of the primary segments, thus establishing a secondary segmentation in which the longitudinal muscles became intersegmental instead of intrasegmental in action. The sclerotized appendages necessarily became segmented into individually movable parts, and their movements became more specifically controlled by body muscles inserted on their bases. The protarthropods retained the annelid structure of the nervous system, and the independence of the first postoral ganglia of the ventral nerve cords. The prostomial appendages (antennules) assumed an anterior position by a forward migration below the eyes, with the result that in the arthropod brain the antennal lobes lie beneath the optic lobes, and the brain takes a vertical position by contrast with the horizontal position of the onychophoran brain. Lateral eyes of the compound type were first developed in the Protarthropoda. Because of the origin of the Protarthropoda from Protonychophora, the protarthropods were equipped with a series of nephridial organs like those of the Onychophora, and their internal reproductive organs were of the onychophoran type. The segmental relations of the genital ducts, however, were subject to mutation, and the position of the gonopores was, therefore, different in different forms, as shown by the highly variable position of the genital outlets in modern arthropods.

The Protarthropoda, having an annelid ancestry, and being directly derived from wormlike protonychophorons by a sclerotization of the integument and a jointing of the appendages, could scarcely take on other than a centipedelike form and structure, though they did not, of course, have the composite head and other specialized features of present-day myriapods. The number of body segments was variable, and potentially large, since the production of new somites in the zone of growth was not limited. The cephalic appendages (antennules) were filamentous, the lateral eyes primitively compound. The body appendages were probably all ambulatory legs with little differentiation among them, each composed of seven segments. The dactylopodites were provided with extensor and flexor muscles arising in the propodites. Aquatic forms probably had branchial epipodites on the coxopodites. Perhaps the majority of the protarthropods lived in shallow water near the ocean shore, where they inhabited the bottom or aquatic plants, but probably also they occurred abundantly in débris along the beach, and very likely some of them were to be found in damp places on the land. The genital openings being on specific body segments, propagation took place by sex mating, though

fertilization of the eggs was probably external. Postembryonic development was anamorphic. The first major diversification of the Protarthropoda gave rise to the ancestors of the Trilobita and the ancestors of the Mandibulata (fig. 54).

10.—The Trilobita preserved the uniform, generalized structure and segmentation of the protarthropod appendages, but otherwise they became highly specialized by a lateral extension of the margins of the body segments, taking on thus a broad, flattened form except for a median elevation giving passage to the alimentary canal. Furthermore, the first four postoral segments became intimately united with one another and with the prostomial acron to form a solid anterior body section, or prosoma, the so-called "head," bearing the labrum, the eyes, the antennules, and four pairs of postoral ambulatory appendages. Basal endites of the anterior appendages may have served as feeding adjuncts, but the trilobites, so far as known, developed no specific jaws. The Trilobita were entirely marine animals, but they lived at the bottom of the water, and their legs show few deviations from the ambulatory type of structure, except for the high development of branchial lobes from the lateral surfaces of the coxopodites. The extended tergal margins covering the gills probably formed respiratory chambers. The position of the genital openings in the trilobites has not been discovered, but, because of the close relation between the Trilobita and the Chelicerata, the genital apertures may be expected to be found on the fourth postcephalic segment. The Trilobita became extinct by the end of the Paleozoic period of geological history, but from a branch of the primitive pre-Cambrian prototrilobites were evolved the Chelicerata.

11.—The Chelicerata are distinguished from the Trilobita by the union of several additional somites with the head to form a more extensive prosoma, by the loss of the acronal appendages (antennules), by a greater differentiation among the somatic appendages, and by the forcipate structure of the reduced first appendages. Very commonly, also, there is an extra podomere in at least some of the legs, the patella, interpolated between the femur and the tibia. In modern forms the nephridial organs are suppressed in most of the somites, but some of them are retained as coxal glands, and (except in Pycnogonida and some Acarinida) the genital openings occur always on the eighth postoral somite. The Chelicerata have become the most sepecialized of all the arthropods, there being little in their body form and general organization suggestive of the ancestral centipede type of structure, which is so evident throughout the mandibulate

branch. The Chelicerata include the Xiphosurida, the Eurypterida, the Arachnida, the Acarinida, and very probably the Pycnogonida.

12.—The Xiphosurida are undoubtedly the closest living representatives of the Trilobita. The xiphosurid prosoma has the same structure as the trilobite head, and the same composition except for the addition of three extra somites and a part of the eighth somite. Likewise, the opisthosoma corresponds with the trilobite pygidium extended forward to include all the somites behind the prosoma, so that in the Xiphosurida there is no intermediate "thoracic" region of free segments. Such fossil forms as *Belinurus* and *Prestwichia* would appear to be intermediate between modern Xiphosurida and Trilobita, and the Middle Cambrian *Naraoia* (see Walcott, 1931, fig. 1) must be related to the xiphosurid line somewhere close to the trilobites. The first six prosomatic appendages retain the leg type of structure, except for the reduction and chelicerate form of the first pair. The seventh appendages are reduced to a pair of small lobes, the chilaria, and the following six have the form of broad plates formed chiefly by epipodite lobes, those of the last five bearing lamellate gills. The genital openings in both sexes are on a median ventral fold of the eighth segment united with the bases of the opercular appendages of this segment.

13.—The Pycnogonida, judging from some of their structural features, such as the union of the anterior body segments, the posterior position of the dorsal eyes between the bases of the third pair of appendages, the presence of a patellar segment in the legs, and the chelicerate structure of the first appendages, are to be classed with the Chelicerata; but because of their many unique characters, including the occurrence of multiple genital openings, it is impossible to connect them closely with any other of the chelicerate groups. It may be noted, however, that species with eight pairs of legs have presumably the same number of somites in the prosoma as have the Xiphosurida.

14.—The Eurypterida and the Arachnida differ from the xiphosurids in having only six segments in the prosoma, and this character together with various other features of their organization shows that these two groups are more closely related to each other than is either group to the Xiphosurida. On the other hand, the Eurypterida have certain characters of the xiphosurids that leave little doubt of their common ancestry with the latter, and their descent from trilobite stock. The general resemblance of the eurypterids to scorpions suggests a relationship between the two, but the theory of Versluys and Demoll (1920, 1923) that the Eurypterida and Xiphosurida are

derived from primitive aquatic scorpions cannot be maintained against the evidence of close relationship between the Xiphosurida and the Trilobita. The Arachnida, as invaders of the land, had to evolve organs for aerial respiration, and the lamellate gills of their aquatic progenitors borne on the abdominal appendages were structures readily convertible into "lung books" by invagination into pockets of the integument (see Lankester, 1885). In addition, however, tracheal ingrowths of the body wall were developed in the Arachnida, as they have been in nearly all the other terrestrial arthropods.

15.—The Protomandibulata preserved the slender, polypodous, centipedelike form of the primitive protarthropods, but they acquired as a distinctive character a pair of jawlike feeding organs, the *mandibles*, developed from the bases of the second postoral appendages. Probably long before the evolution of the mandibles, the first somite had been united with the prostomial acron to form a primitive composite head, or protocephalon, bearing the acronal sensory organs, the mouth, and the first pair of postoral appendages, which last became a second pair of antennae. The two pairs of appendages following the mandibles were reduced and modified to serve as accessory feeding organs. The other appendages were probably all leglike in form, as in modern centipedes, and were 7-segmented, since a patella does not occur in the mandibulate branch of the arthropods. The circulatory system still retained the basic structure of that of the generalized annelids; respiration probably was branchial, the gills being carried on epipodite lobes of the coxopodites, as in the Trilobita; the nephridial organs were perhaps suppressed in most of the body segments, but those that remained were of the onychophoran type of structure. The reproductive organs were closed gonadial tubes opening in each sex through a single pair of ducts formed from a pair of coelomic sacs, but the segmental position of the genital openings varied in different forms according to what particular pair of coelomic sacs served as gonadial outlets.

The primitive Protomandibulata probably inhabited both the water and the land, since from them were early evolved the aquatic Crustacea, while the main branch developed into the terrestrial Protomyriapoda, from which have descended the modern myriapods and the Hexapoda.

16.—That the Crustacea are derived from crawling, centipedelike protomandibulate ancestors is attested by the retention in all the higher forms of ambulatory appendages having the same structure as the limbs of terrestrial arthropods. Many forms, however, have become adapted in part or entirely to swimming by a modification of the

appendages, and the special development of an exite lobe of the basipodites has given rise to a characteristic biramous structure of the limbs. The primitive protocephalon is retained as the definitive head in the Anostraca and in most of the Malacostraca, but in the majority of the Entomostraca and in the Leptostraca, Amphipoda, and Isopoda from three to five gnathal somites have been united with the protocephalon to form a more extensive cephalic structure. A carapace is variously developed in many groups, either from the cephalognathal region, or from the gnathothoracic region, but there is no true cephalothorax formed by an intimate union of cephalic and thoracic somites as in the Chelicerata. The mandibles have no movable lobes such as those of the myriapods; in most forms the jaws preserve the primitive monocondylic articulation with the head, but in the higher Malacostraca they are secondarily dicondylic. The genital openings are variable in position in the Entomostraca, but are fixed with respect to a specific segment in the Malacostraca. The hatching of the young at an early embryonic stage has resulted in the development of specialized swimming larval forms representing more primitive ancestral stages in their general structure than the immediate protarthropod ancestors of the crustaceans. The great antiquity of the Crustacea is shown by the occurrence of highly evolved forms in the Cambrian period contemporaneous with the oldest known trilobites.

17.—The Protomyriapoda, being the direct descendants of the protarthropods, perpetuated the generalized arthropod form after the trilobites, the chelicerates, and the crustaceans had branched off as side issues and taken on variously specialized forms. During their evolution the protomyriapods acquired the structures characteristic of their descendants, which include the modern Symphyla, Diplopoda, Hexapoda, and Chilopoda. The three gnathal somites became intimately united with one another and with the protocephalon, forming the standardized head of the above-mentioned groups, composed of the acron and four postoral segments. The compound eyes and the first antennae of the Protomandibulata were retained, but the second antennae became reduced and eventually were lost, though their ganglia were preserved as tritocerebral lobes of the brain. The mandibles lost the telopodites, but each had a strong gnathal lobe (lacinia) movable by a muscle arising within the coxopodite and by another arising on the cranial wall. The two postmandibular maxillary appendages were modified by a reduction of the telopodites and by other adaptations to serve as accessory feeding organs. Since the Symphyla and some of the more generalized Hexapoda have lateral hypopharyngeal lobes (superlinguae) resembling the paragnatha of

Crustacea, it is possible that these structures were transmitted from the Crustacea to the symphylids and hexapods through the Protomyriapoda, though they have been lost in modern Diplopoda and Chilopoda. The legs of the protomyriapods were all alike and retained the generalized 7-segmented structure, but the extensor muscle of the pretarsus was lost, leaving only the flexor muscle, which, for more effective action, shifted its origin from the tarsus into more proximal segments of the leg. This last feature is a distinctive character of all the descendants of the Protomyriapoda. Nephridial excretory organs were supplemented or replaced functionally by Malpighian tubules of the proctodaeum. The position of the genital openings was probably in general posterior, but variable. Postembryonic development was anamorphic, the young being hatched with a small number of segments, and the full number acquired by teloblastic generation in the subterminal zone of growth.

The Protomyriapoda undoubtedly were terrestrial, and the larger forms may have developed tracheal invaginations on various parts of the body for respiration, but there was no definitely established tracheal system transmitted alike to all the descendent groups of terrestrial mandibulates. The probable characters of the Protomyriapoda are summarized as follows by Imms (1936):

(1) The head bore a single pair of antennae and two pairs of jaws, viz. mandibles and maxillae: the second maxillae were probably a subsequent acquisition. (2) The trunk was composed of a variable and indefinite number of sub-equal segments, each bearing a pair of legs. It is probable that anamorphosis was universal and was continued throughout the life of the animal. (3) The gonads opened to the exterior by paired apertures, and the segmental disposition of the orifices probably varied in different families and depended upon that of the coelomoducts involved. . . . (4) The alimentary canal was probably a simple straight tube, while the excretory organs were little more than proctodaeal outgrowths or pockets; an accessory excretory function was probably performed by the fat-body. (5) Respiration was probably cutaneous in many forms and partially tracheate in others. The tracheae were presumably in the form of groups of unbranched tubuli devoid of taenidia and bearing a general resemblance to those of Diplopoda. Each group of tracheae opened laterally by means of simple cryptlike, segmentally arranged spiracles: in some forms a pair of spiracles was probably located also on the head.

From the Protomyriapoda there emerged a specialized lateral branch, the Protosymphyla, from which have been evolved in one direction the progoneate modern Symphyla, Pauropoda, and Diplopoda, in another the opisthogoneate Hexapoda, while the generalized myriapodan stock has more directly continued into the modern Chilopoda.

18.—Since modern Symphyla combine features of the progoneate Diplopoda and Pauropoda on the one hand, and of the opisthogoneate Hexapoda on the other, there can be little question that they are direct descendants of common ancestors of these two groups. Modern Symphyla, however, are linked more closely with the progoneate forms by the anterior position of the gonopore, the segmentation and structure of the legs, and the retention of the movable laciniae of the mandibles. The Protosymphyla, therefore, gave rise to an opisthogoneate branch that became the Protohexapoda.

In general appearance the Protosymphyla probably resembled their modern representatives, but retained certain features of the Protomyriapoda that have been transmitted to the hexapod line, though lost in the progoneate descendants. The legs were all alike and had the 7-segmented protomyriapod type of structure, but the coxopodites bore each, mesad of the telopodite base, a small stylus and an eversible vesicle, as in modern Symphyla (fig. 52 H), which structures are preserved also on the abdomen of some of the apterygote insects (I). The appendages of the last body somite became reduced to styliform cerci. The head appendages included a pair of antennae, a pair of mandibles, and two pairs of maxillae. The lateral eyes must have been compound, because compound eyes have been transmitted along the arthropod line from the Trilobita to the Xiphosurida, the Crustacea, and through the Protosymphyla to the Hexapoda. The protosymphylan mandibles had the protomyriapodan structure, movable laciniae being well developed, and palpi absent. The first and second maxillae retained the palpi and each acquired two basal lobes (lacinia and galea), features transmitted to the hexapods, though the palpi have been lost in the progoneate branch. The bases of the second maxillae, however, became united to form a single appendage, the *labium*, an organ so characteristic of all the descendants of the Protosymphyla that the group as a whole, including Symphyla, Pauropoda, Diplopoda, and Hexapoda, might well be designated the "Labiata" (fig. 54).

19.—The direct descendants of the progoneate branch of the protosymphylids are the modern Symphyla, but at an early period there were evolved from the symphylid line the common ancestors of the Diplopoda and Pauropoda. The Symphyla retain the generalized structure of the body and appendages (fig. 52 A), but of the 16 body segments evident in the dorsum of most forms, 3 are without appendages. The legs (K) show the diplopod type of structure in the relatively large size of the second trochanter (*2Tr*) and the smallness of the femur (*Fm*), but the coxae do not appear as typical leg segments, since each pair apparently is confluent in a large posterior division of

the venter of the body segment (H, Cr), carrying mesad of the base of each telopodite a small stylus (*Sty*) and an eversible vesicle (*Vs*). The end segments of the legs are reduced to small dactyls (K, *dac*), but each has an accessory claw (*un*) arising from its base. The first legs are usually reduced in size and lack tibiae. The last body segment bears a pair of cerci (L, *Cer*), which presumably are homologues of the legs or possibly of the styli of the preceding segments. Compound eyes are absent. The mandibles preserve the movable laciniae (E, *Lc*); the maxillae have both laciniae and galeae (B), but the palpi are small or vestigial; the labium (C) is a simple flap without palpi. Lateral lobes of the hypopharynx (superlinguae) are present at least in *Scutigere*lla, as shown by Hansen (1930), and a pair of slender apodemal arms extend into the head from the hypopharyngeal base. The single median genital aperture is situated on the anterior part of the venter of the fourth body segment, but since the paired gonopores of Pauropoda and Diplopoda are on the third body segment, the median genital outlet of the symphylids might be supposed to have migrated secondarily into the fourth segment.

20.—The Diplopoda are a specialized branch of the early Symphyla, in which the somites back of the fourth postcephalic somite are united in pairs to form double segments. The mandibles are well developed and have strong movable lacinial lobes, but there is only one post-mandibular appendage of the head, the gnathochilarium (fig. 52 G), the morphology of which is uncertain, though the organ is probably either a combination of the maxillae with the labium, or the labium alone. The legs of the first body segment are absent, and there are no cerci on the last somite. Body segments are numerous in most forms, and all but the first few are generated teloblastically in pairs during postembryonic development. The paired gonopores are on the third postcephalic somite at the bases of the second pair of legs. The Pauropoda are probably an early branch of the Diplopoda, in which a union of the somites in pairs had already taken place, and the first legs had been much reduced but not yet obliterated. Special characters of the pauropods are the lack of movable laciniae on the mandibles, a weak development of the gnathochilarium, and a branching of the antennae beyond the fourth segments.

21.—The Hexapoda resemble more closely the Symphyla than any other of the modern arthropods, a fact recognized by several of the earlier writers, and Packard (1898) first formulated a definite theory of the origin of insects from symphylid ancestors. Recently the evidence in favor of this theory has been more thoroughly reviewed in the light of present-day knowledge of the apterygote hexapods by

Inms (1936), who shows that the most plausible concept of the ancestry of insects is that of symphylid derivation. The important difference between modern Hexapoda and Symphyla is in the position of the genital openings, the symphylids being progoneate, the hexapods opisthgoneate. It is necessary to assume, therefore, that the Protohexapoda were evolved from an opisthgoneate branch of the Protosymphyla.

The Protohexapoda became differentiated as a hexapod group through the concentration of the locomotor function in the first three postcephalic segments, with the consequent division of the body into a motor thorax and a visceral abdomen. The abdominal appendages were reduced, modified for purposes other than locomotion, or suppressed, but in most cases the abdominal coxal remnants united with the sternal plates of the segments and preserved the styli and eversible vesicles inherited from the Protosymphyla, though on the thorax these structures were lost. The number of body segments was limited to 14 somites and a simple terminal lobe (telson) containing the anus. The persistent appendicular organs of the last somite were styluslike cerci, as in Symphyla. It is probable that the true telopodites of all the abdominal segments were absent. The mandibles became solid jaws by a complete fusion of the lacinial lobes with the coxopodites, and thus came to resemble the mandibles of Crustacea, but the maxillae and labium retained the generalized protosymphylan structure. The hypopharynx consisted of a median lobe and two lateral lobes, as in Symphyla, and had a pair of basal apodemes giving attachment to muscles of the gnathal appendages. The eyes were compound. The protohexapods were opisthgoneate insofar as the paired genital apertures were located on the posterior part of the abdomen, but the exact position of the ducts and their outlets was still subject to mutation, as shown in the variable position of the genital outlets in modern forms.

The discrepancy in the position of the genital openings as between Symphyla and Hexapoda raises the chief difficulty in relating the hexapods directly to the symphylids. The opisthgoneatism of the Hexapoda, however, is more truly a heterogoneate condition, which in a broad sense applies to the entire group of labiate mandibulates, for the primary genital ducts open on the third postcephalic somite in Diplopoda and Pauropoda, on the eighth in Collembola, on the tenth in female Pterygota, on the thirteenth (primitively) in male Pterygota, and on the fourteenth in Protura. Since the primary gonopores of the hexapods are always fixed with specific segments, as in Symphyla, Pauropoda, and Diplopoda, the opisthgoneate con-

dition in the Hexapoda is not comparable with that in the Chilopoda, in which the genital outlet, though always subterminal, may be on a quite different somite in different forms because of the variable number of somites that may precede it. There is reason for believing, therefore, that the opisthogoneate condition of the Hexapoda has been acquired secondarily, and that it is a derivative from the progoneatism of Symphyla and Diplopoda, rather than from the opisthogoneatism of Protomyriapoda represented in modern Chilopoda. The establishment of the genital openings on the posterior part of the body in the Hexapoda was very probably an adaptation correlated with the concentration of the locomotor function in the thorax.

22.—An early specialization among the Protohexapoda gave rise to the modern entognathous Diplura, Protura, and Collembola, small hexapods characterized by a retraction of the mandibles and maxillae into pouches of the head wall closed ventrally by the labium. The identity in the structure of the mouth parts would alone suggest a phylogenetic unity among the above-mentioned groups, but the latter show also a peculiarity in the development of the hypopharyngeal apodemes, which structures, instead of projecting as free arms into the head, as in myriapods and Machilidae, take the form of long internal ridges that, in Diplura and Collembola, diverge posteriorly from the base of the hypopharynx as sclerotic linear inflections of the membranous integument along the folds between the gnathal pouches and the inner surface of the labium. In Protura the two rods are united for a part of their length. These superficial apodemes give attachment to the same muscles as do the internal apodemes of other forms, and in Collembola they support an elaborate "tentorial" superstructure. In many other respects the entognathous hexapods are widely different from one another, and their inter-relationships are by no means clear. Except for the common characters above mentioned, they might be supposed to have had quite separate origins from protosymphylan or protohexapod ancestors (see Imms, 1936, fig. 11). They represent abortive lines of evolution that have not led to higher forms.

The Diplura depart least from the thysanuran branch that has given rise to the winged insects, since they retain the abdominal styli and cerci, and have the usual hexapod position of the genital openings. The Protura preserve a remnant of the primitive anamorphism of the hexapod ancestors, inasmuch as the last two somites are formed during postembryonic development, but they lack antennae, styli, and cerci; the small appendicular organs on the first three abdominal segments may be coxal remnants of limbs, with eversible vesicles in

one family. The paired genital ducts in both sexes open on the eleventh abdominal segment. The Collembola are the most aberrant of all the hexapods, and in some ways the most primitive. They have only nine body segments, and the single genital opening is on the fifth abdominal segment. There can be no question that the Collembola are derived from more generalized ancestors having a greater number of segments, but since, in their phylogenetic history, segment formation in the zone of growth has ceased after the establishment of the genital ducts in the eighth somite, it is fruitless to look for evidence of the ancestral segmentation in the embryogeny of present-day Collembola. The three pairs of appendicular organs on the collembolan abdomen are unique in structure, and give little suggestion of homology with the abdominal appendages of Symphyla, Diplura, and Thysanura, though it may be supposed that the collophore is a pair of united eversible vesicles, and that the two paired appendages are highly developed styli. (For a fuller discussion of the special features of the Collembola, see Imms, 1936.)

23.—The main evolutionary line of the early hexapods led from the opisthogoneate branch of the Protosymphyla directly into the Machilidae, since in this family are best preserved the coxal accessory structures of the symphylids (fig. 52 I) along with the normal ectognathous mouth parts. Moreover, it was in the ancestors of the Machilidae that the characteristic ovipositor of the hexapods had its inception, and, therefore, from the machilid line have been evolved the Lepismatidae and the Pterygota. The common ancestors of these last two groups developed two special features in the head structure. One was the acquisition of a secondary anterior articulation of the mandible on the cranium, giving the jaw a hinge movement on a longitudinal axis, which brought about a reorganization of the mandibular musculature, giving the principal function of abduction and adduction to the dorsal muscles, and reducing the ventral muscles to a condition of such little importance that they have completely disappeared in the higher Pterygota. The other feature was the development of the endocranial framework known as the tentorium, characteristically present in Lepismatidae and Pterygota, but foretokened in Machilidae. The tentorium is evidently a product of the hypopharyngeal apodemes and of a transverse bar developed in the back of the head from lateral invaginations. Both structures are present in Machilidae, but are not united. In Lepismatidae the anterior apodemes are reflected directly from the cranial margins and are united posteriorly with the transverse bar, producing a typical tentorium. In the Pterygota the roots of the anterior arms take a submarginal position on the cranium, and in higher forms they have migrated to the facial aspect of the head.

The hexapod structure, with the locomotor function centered in the thorax, apparently gave little if any advantage over the polypod structure for ordinary terrestrial life, but it furnished a condition particularly fitted for the development of wings. Hence, with the appearance of alar lobes on the thorax, the evolution of these lobes into organs of flight was readily accomplished, and the pterygote insects quickly achieved a great superiority over the other arthropods. While there is much to suggest that the winged insects are most closely related to the apterygote thysanurans, their direct origin from the latter is questionable. It is difficult to explain, for example, how it comes about that the pterygote Ephemeroptera and Dermaptera have paired genital openings while secondary median ducts are already established in the Thysanura, with openings on the same segments as in the higher Pterygota.

24.—The Chilopoda are the conservatives among the arthropods; they are the least-modified descendants of the Protomyriapoda, and in certain phases of their embryogeny they still follow the course of development in the Onychophora. The gnathal appendages are probably more generalized than in any other of the Mandibulata; though the bases of the mandibles are deeply sunken into pouches of the head wall, they have strongly muscled lacinial lobes (fig. 53 E, F), and the two maxillary appendages (C) are but little modified except by reduction of the telopodites and a partial union of the coxopodites. The suspensorial sclerites of the hypopharynx maintain connections with the cranial margins, and bear the apodemes on which the ventral muscles of the gnathal appendages are attached. The characteristic specialization of the chilopods is the conversion of the first legs into a pair of poison claws (B). Most of the other body appendages retain the structure of simple 7-segmented legs, though at the base of each is an extensive subcoxal sclerotization suggestive of that in the insect thorax. The last two pairs of legs are reduced and modified to serve as genital accessories, and consequently there are no terminal cerci. Styli and eversible vesicles are absent. The genital opening is always on the last somite before the telson, but since the total number of somites is variable, the genital segment may be a quite different somite in different chilopod groups. Anamorphic postembryonic development persists in some forms, while in others segmentation is complete at hatching.

25.—Evolution may be accepted as a fact, but the true history of phylogeny can never be demonstrated. Though the main branches of the genealogic tree of any major group of animals are fairly evident, an endeavor to follow in detail the phylogenetic connections between more closely related forms invariably leads into a maze of difficulties,

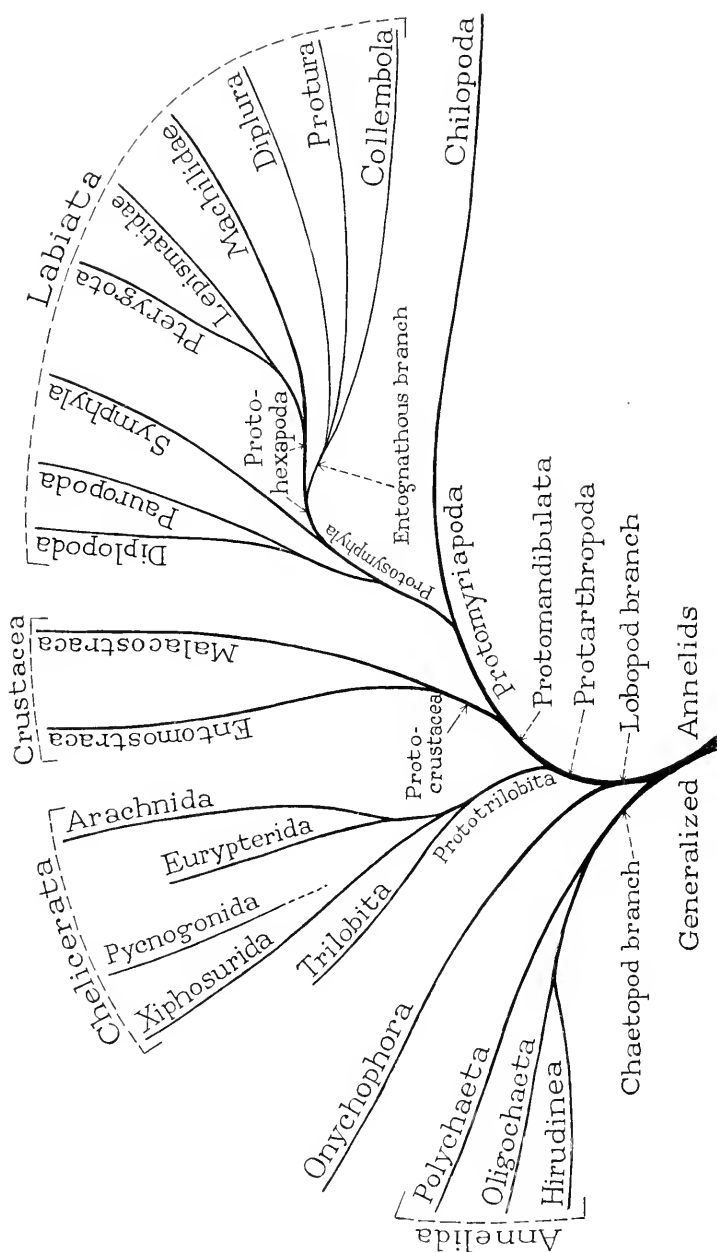


FIG. 54.—Diagram illustrating the phylogenetic relationships of the Annelida, Onychophora, and Arthropoda proposed in the text.

for it is seldom found that all characters will fit into a scheme of relationship that attempts to relate every feature in one form with a similar feature in another. It must be recognized that various structural adaptations have been often independently developed in approximately the same way. A successful adaptation will be equally valuable in many groups, and it is, therefore, not surprising that an adaptive structure should independently recur either in distantly related or in closely related groups. To distinguish between such structures and those that have had an identical origin, however, is one of the most uncertain tasks of the phylogeneticist, but the very condition of uncertainty injects into the study of phylogeny the element of personal opinion which gives to phylogeny that controversial status by which it never lacks in interest. Every biologist must have a working creed of phylogeny, but he should not too implicitly believe its tenets.

REFERENCES

BADEN, V.

1936. Embryology of the nervous system in the grasshopper, *Melanoplus differentialis* (Acrididae; Orthoptera). *Journ. Morph.*, vol. 60, pp. 159-188, 4 pls.

BALFOUR, F. M.

1880. Notes on the development of the Araneina. *Quart. Journ. Micr. Sci.*, vol. 20, pp. 1-23, pls. 19-21.
1883. The anatomy and development of *Peripatus capensis*. *Quart. Journ. Micr. Sci.*, vol. 23, pp. 213-259, pls. 13-20.

BENHAM, W. B. S.

1885. Description of the muscular and endoskeletal systems of *Limulus*. *Trans. Zool. Soc. London*, vol. 11, pp. 314-338, pls. 72-76. (See Lankester, Benham, and Beck, 1885.)

BERGH, R. S.

1888. Zur Bildungsgeschichte der Excretionsorgane bei *Criodrilus*. *Arb. Zool.-Zoot. Inst. Würzburg*, vol. 8, pp. 223-248, pls. 13, 14.
1890. Neue Beiträge zur Embryologie der Anneliden. I. Zur Entwicklung und Differenzierung des Keimstreifens von *Lumbricus*. *Zeitschr. wiss. Zool.*, vol. 50, pp. 469-526, pls. 19-21.
1899. Nochmals über die Entwicklung der Segmentalorgane. *Zeitschr. wiss. Zool.*, vol. 66, pp. 435-449, pl. 30.

BIGELOW, M. A.

1902. The early development of *Lepas*. A study of cell-lineage and germ-layers. *Bull. Mus. Comp. Zoöl.*, vol. 40, pp. 61-144, 12 pls.

BINARD, ALICE, and JEENER, R.

1926. Recherches sur la morphologie du système nerveux des Annélides. I. *Nereis*. *Bull. Acad. R. Belgique, Classe Sci.*, ser. 5, vol. 12, pp. 437-448, 6 figs.
1928. Sur l'existence de cavités coelomiques dans le segment palpaire des Polychètes. *Recueil Inst. Zool. Torley-Rousseau*, vol. 1, pp. 173-178, 1 fig.
1929. Morphologie du lobe préoral des Polychètes. *Recueil Inst. Zool. Torley-Rousseau*, vol. 2, pp. 117-240, 45 text figs., pls. 5-12.

BOUVIER, E. L.

1902. Sur l'organisation, le développement et les affinités du *Peripatopsis Blainvillei* Gay-Gervais. Zool. Jahrb., Suppl. vol. 5 (Fauna Chilensis, vol. 2), pp. 675-730, pls. 20-22.

1905, 1907. Monographie des Onychophores. Ann. Sci. Nat., Zool. sér. 9, vol. 2, pp. 1-383, pls. 1-13; vol. 5, pp. 61-318, 191 figs.

BRACE, EDITH M.

1901. Notes on *Aeolosoma tenebrarum*. Journ. Morph., vol. 17, pp. 177-184, pl. 21.

BRAUER, A.

1895. Beiträge zur Kenntnis der Entwicklungsgeschichte des Skorpions. II. Zeitschr. wiss. Zool., vol. 59, pp. 351-435, 20 text figs., pls. 21-25.

BRUNTZ, L.

1903. Sur la présence des reins labiaux et d'un organ phagocytaire chez les Diplopodes. C. R. Acad. Sci. Paris, vol. 136, pp. 57-59.

1908. Les reins labiaux et les glandes céphaliques des Thysanoures. Arch. Zool. Exp. Gén., vol. 9, pp. 195-238, pls. 2, 3.

BÜRGER, O.

1891. Beiträge zur Entwicklungsgeschichte der Hirudineen. Zur Embryologie von *Nepheleis*. Zool. Jahrb., Anat., vol. 4, pp. 697-738, pls. 41-43.

1894. Neue Beiträge zur Entwicklungsgeschichte der Hirudineen. (*Hirudo* and *Aulastomum*). Zeitschr. wiss. Zool., vol. 58, pp. 440-459, pls. 26-28.

BUXTON, B. H.

1913. Coxal glands of the arachnids. Zool. Jahrb., Suppl. 14, pp. 231-282, pls. 1-43.

1917. Notes on the anatomy of arachnids. Journ. Morph., vol. 29, pp. 1-31, 8 text figs., 3 pls.

BYCHOWSKY, A.

1921. Über die Entwicklung der Nephridien von *Clepsine sexoculata* Bergmann. Rev. Suisse Zool., vol. 29, pp. 41-131, 16 text figs., pls. 1-5.

CAMERANO, L.

1897. Sulla striatura trasversale dei muscoli delle mandibole negli Onicofori. Atti R. Accad. Sci. Torino, vol. 33, pp. 589-593.

CANNON, H. G., and MANTON, S. M.

1927. Notes on the segmental excretory organs of Crustacea. I-IV. Journ. Linn. Soc. London, vol. 36, pp. 439-456, 7 figs.

CHICKERING, A. M.

1937. Evolution in spiders. 38th Ann. Rep., Michigan Acad. Sci., Arts, Lett., pp. 22-51.

CHILD, C. M.

1900. The early development of *Arenicola* and *Sternaspis*. Arch. Entw. mech., vol. 9, pp. 587-723, pls. 21-25.

CRAMPTON, G. C.

1928. The evolution of insects, chilopods, diplopods, Crustacea, and other arthropods indicated by a study of the head capsule. Canadian Ent., vol. 60, pp. 129-141, pls. 8-12.

1928. The evolution of the head region in lower arthropods and its bearing upon the origin and relationships of the arthropodan groups. Canadian Ent., vol. 60, pp. 284-301, pls. 20, 21, 22.

CUÉNOT, L.

1926. L'entonnoir vibratile de la néphridie des Péripatés. Ann. Soc. R. Zool. Belgique, vol. 56, pp. 13-17.

CURTIS, W. C., and GUTHRIE, MARY J.

1927. Textbook of general zoology. New York and London.

DAKIN, W. J.

1920. Fauna of Western Australia. III. Further contributions to the study of the Onychophora. Proc. Zool. Soc. London, vol. for 1920, pp. 367-389, 5 pls.
1921. The eye of Peripatus. Quart. Journ. Micr. Sci., vol. 65, pp. 163-171, 3 text figs., pl. 7.

DAUTERT, E.

1929. Die Bildung der Keimblätter von Paludina vivipara. Zool. Jahrb., Anat., vol. 50, pp. 433-496, 33 figs.

EISIG, H.

1899. Zur Entwicklungsgeschichte der Capitelliden. Mitt. Zool. Sta. Neapel, vol. 13, pp. 1-292, pls. 1-9.

EVANS, R.

1902. On the Malayan species of Onychophora. Part II. The development of Eoperipatus weldoni. Quart. Journ. Micr. Sci., vol. 45, pp. 41-88, pls. 5-9.

FAHLANDER, K.

1938. Beiträge zur Anatomie und Systematischen Einteilung der Chilopoden. Zool. Bidrag Uppsala, vol. 17, pp. 1-148, 36 text figs., 18 pls.

FAUSSEK, V.

1899. Über die physiologische Bedeutung des Coeloms. Trav. Soc. Imp. Nat. St. Petersburg, vol. 30, Livr. 1, pp. 40-57 (in Russian), 83-84 (résumé in German).
1901. Untersuchungen über die Entwicklung der Cephalopoden (VII, Was ist das Cölom?). Mitt. Zool. Station Neapel, vol. 14, pp. 83-237, pls. 6-10.

FEDOROW, B.

1926. Zur Anatomie des Nervensystems von Peripatus. I. Das Neurosomit von Peripatus tholloni Bouv. Zool. Jahrb., Anat., vol. 48, pp. 273-310, 4 text figs., pls. 10, 11.
1929. Zur Anatomie des Nervensystems von Peripatus. II. Das Nervensystem des vorderen Körperendes und seine Metamerie. Zool. Jahrb., Anat., vol. 50, pp. 279-332, pls. 6, 7.

GLEN, EDITH H.

1919. A revision of certain points in the early development of Peripatus capensis. Quart. Journ. Micr. Sci., vol. 63, pp. 283-292, pl. 20.

GOODRICH, E. S.

- 1898-1900. On the nephridia of the Polychaeta. Parts I-III. Quart. Journ. Micr. Sci., vol. 40, pp. 185-195, pls. 6-9; vol. 41, pp. 439-457, pls. 32-35; vol. 43, pp. 699-748, pls. 37-42.
1912. Nerilla an archianellid. Quart. Journ. Micr. Sci., vol. 57, pp. 397-425, pls. 38-41.

GUILDING, L.

1826. Molusca Carribeana. 2. An account of a new genus of Mollusca. Zool. Journ., vol. 2, pp. 437-444, pl. 14.

GUSTAFSON, G.

1930. Anatomische Studien über die Polychäten-Familien Amphinomidae und Euphrosynidae. Zool. Bidrag Uppsala, vol. 12, pp. 305-471, 64 text figs., 36 pls.

HACKER, V.

1895. Die spätere Entwicklung der Polynoë-Larve. Zool. Jahrb., Anat., vol. 8, pp. 245-288, pls. 14-17.

HAMAKER, J. I.

1898. The nervous system of *Nereis virens* Sars. Bull. Mus. Comp. Zoöl., vol. 32, pp. 89-124, 5 pls.

HANSEN, H. J.

1930. Studies on Arthropoda III. Copenhagen.

HANSTRÖM, B.

1926. Eine genetische Studie über die Augen und Schzentren von Turbellarien, Anneliden und Arthropoden. K. Svenska Vetenskapsakad. Handl., 3d ser., vol. 4, no. 1, 176 pp., 80 figs.
1927. Das zentrale und periphere Nervensystem des Kopflappens einiger Polychäten. Zeitschr. Morph. Ökol. Tiere, vol. 7, pp. 543-596, 27 figs.
1928. Vergleichende Anatomie des Nervensystems der wirbellosen Tiere. Berlin.
1929. Weitere Beiträge zur Kenntnis des Gehirns und der Sinnesorgane der Polychäten. Zeitschr. Morph. Ökol. Tiere, vol. 13, pp. 329-358, 27 figs.
1935. Bemerkungen über das Gehirn und die Sinnesorgane der Onychophoren. Lunds Univ. Årssk. N. F. Avd. 2, vol. 31, no. 5, 38 pp., 22 figs.

HATSCHEK, B.

1877. Die Embryonalentwicklung und Knospung von *Pedicellina echinata*. Zeitschr. wiss. Zool., vol. 29, pp. 502-549, pls. 28-30.
- 1888-91. Lehrbuch der Zoologie. Jena.
1894. Über den gegenwärtigen Stand der Keimblättertheorie. Verh. Deutschen Zool. Ges. 3d Jahresvers., pp. 11-23.

HEATHCOTE, F. G.

1886. The early development of *Julus terrestris*. Quart. Journ. Micr. Sci., vol. 26, pp. 449-470, pls. 23, 24.

HEIDER, K.

1925. Über Eunice. Systematisches, Kiefersack, Nervensystem. Zeitschr. wiss. Zool., vol. 125, pp. 55-90, 16 figs.

HEMPELMANN, F.

1911. Zur Naturgeschichte von *Nereis dumerilii* Aud. et Edw. Zoologica. Orig.-Abhandl. Gesamtg. Zool., vol. 62, 135 pp., 4 pls.
1931. Archiannelida and Polychaeta. Kükenthal and Krumbach's Handbuch der Zoologie, vol. 2, 2d half.

HENRIKSEN, K. L.

1926. The segmentation of the trilobite's head. Saert. Meddel. Dansk Geol. For., vol. 7, pp. 1-32, 27 figs.
1929. Contribution to the interpretation of the cephalic segments of Arthropoda. Trans. 4th Internat. Congr. Ent. (Ithaca, N. Y.), pp. 589-594.

HERTWIG, O. and R.

1882. Die Cölomtheorie, Versuch einer Erklärung des mittleren Keimblattes. *Jenaische Zeitschr. Naturwiss.*, vol. 15 (N. F. vol. 8), pp. 1-150, 3 pls.

HESS, W. N.

1925. Nervous system of the earthworm, *Lumbricus terrestris* L. *Journ. Morph.*, vol. 40, pp. 235-259, 7 figs.

HESSE, R.

1899. Untersuchungen über die Organe der Lichtempfindung bei niederen Thieren. V. Die Augen der polychäten Anneliden. *Zeitschr. wiss. Zool.*, vol. 65, pp. 446-516, pls. 22-26.

HESSE, R., ALLEE, W. C. and SCHMIDT, K. P.

1937. *Ecological animal geography*. New York and London.

HEYMONS, R.

1897. Mittheilungen über Segmentirung und den Körperbau der Myriapoden. *Sitzungsbr. K. Preuss. Akad. Wiss. Berlin*, vol. for 1897, pp. 915-923, 2 figs.

1901. Die Entwicklungsgeschichte der Scolopender. *Zoologica. Orig.-Abhandl. Gesammtg. Zool.*, vol. 33, 244 pp., 42 text figs., 8 pls.

1928. Über Morphologie und verwandtschaftliche Beziehungen des *Xenusion auerswaldae* Pomp. aus dem Algonkium. *Zeitschr. Morph. Ökol. Tiere*, vol. 10, pp. 307-329, 7 figs.

HOLMGREN, N.

1916. Zur vergleichenden Anatomie des Gehirns von Polychaeten, Onychophoren, Xiphosuren, Arachniden, Crustaceen, Myriopoden und Insekten. *K. Svenska Vetenskapsakad. Handl.*, vol. 56, no. 1, 303 pp., 12 pls.

HUTCHINSON, G. E.

1930. Restudy of some Burgess shale fossils. *Proc. U. S. Nat. Mus.*, vol. 78, pp. 1-24, pl. 1.

IMMS, A. D.

1936. The ancestry of insects. *Trans. Soc. British Ent.*, vol. 3, pp. 1-32, 11 figs.

IWANOFF, P. P.

1928. Die Entwicklung der Larvalsegmente bei den Anneliden. *Zeitschr. Morph. Ökol. Tiere*, vol. 10, pp. 62-161, 40 text figs., pls. 1-7.

1933. Die embryonale Entwicklung von *Limulus moluccanus*. *Zool. Jahrb., Anat.*, vol. 56, pp. 163-348, 78 text figs., pls. 1-3.

JANET, C.

1899. *Essai sur la constitution morphologique de la tête de l'insecte*, 74 pp., 7 pls. Paris.

JAWOROWSKI, A.

1891. Über die Extremitäten bei den Embryonen der Arachniden und Insekten. *Zool. Anz.*, vol. 14, pp. 164-169, 173-176, 4 figs.

JEENER, R.

1928. *Recherches sur le système neuromusculaire latéral des Annélides*. *Recueil Inst. Zool. Torley-Rousseau*, vol. 1, pp. 99-121, pl. 3.

KENNEL, J. VON

- 1884, 1888. *Entwicklungsgeschichte von Peripatus Edwardsii* Blanch. und *Peripatus torquatus* n. sp. *Arb. Zool.-Zootom. Inst. Würzburg*, vol. 7, pp. 95-229, pls. 5-11; vol. 8, pp. 1-93, pls. 1-6.

KISHINOUE, K.

1893. On the development of *Limulus longispina*. Journ. Coll. Sci. Imp. Univ. Japan, vol. 5, pp. 53-100, pls. 5-11.

1894. Note on the coelomic cavity of a spider. Journ. Coll. Sci. Imp. Univ. Japan, vol. 6, pp. 287-296, pl. 10.

KLEINENBERG, N.

1886. Die Entstehung des Annelids aus der Larve von *Lopadorhynchus*. Zeitschr. wiss. Zool., vol. 44, pp. 1-227, pls. 1-16.

KOWALEVSKY, A., and MARION, A. F.

1883. Documents pour l'histoire embryogénique des Alcyonaires. Ann. Mus. Hist. Nat. Marseille, Zool., vol. 1, no. 4, 50 pp., 5 pls.

KÜHNERT, L.

1935. Beitrag zur Entwicklungsgeschichte von *Alcippe lampas* Hancock. Zeitschr. Morph. Ökol. Tiere, vol. 29, pp. 45-78, 24 figs.

LALICKER, C. G.

1935. Larval stages of trilobites from the Middle Cambrian of Alabama. Journ. Paleontol., vol. 9, pp. 394-399, pl. 47.

LAMEERE, A.

1926. Les organes segmentaires des Polychètes. Ann. Soc. R. Zool. Belgique, vol. 56, pp. 113-119.

LANKESTER, E. R., BENHAM, W. B. S., and BECK, E. J.

1885. On the muscular and endoskeletal systems of *Limulus* and *Scorpio*, with some notes on the anatomy and generic characters of scorpions. Trans. Zool. Soc. London, vol. 11, pp. 311-384, pls. 72-83.

LILLIE, R. S.

1906. The structure and development of the nephridia of *Arenicola cristata* Stimpson. Mitt. Zool. Sta. Neapel, vol. 17, pp. 341-405, pls. 22-25.

MALAQUIN, A.

1924. Les glandes génitales et les cellules sexuelles primordiales chez l'Annélide *Salmacina Dysteri* (Huxley). La genèse des ébauches génitales par des gonocytes extracoelomiques. C. R. Acad. Sci. Paris, vol. 179, pp. 1348-1351.

1924 a. Les glandes génitales et les cellules sexuelles primordiales chez l'Annélide *Salmacina Dysteri* (Huxley). La filiation des cellules sexuelles (gonocytes); leur origine dans le bourgeon caudal. C. R. Acad. Sci. Paris, vol. 179, pp. 1636-1639.

1925. La ségrégation, au cours de l'ontogénèse, de deux cellules sexuelles primordiales, souches de la lignée germinale, chez *Salmacina Dysteri* (Huxley). C. R. Acad. Sci. Paris, vol. 180, pp. 324-327, 1 fig.

MANTON, S. M.

1928. On the embryology of a mysid crustacean, *Hemimysis lamornae*. Philosoph. Trans. R. Soc. London, ser. B, vol. 216, pp. 363-463, 32 text figs., pls. 21-25.

1930. Notes on the segmental excretory organs of Crustacea. V. On the maxillary glands of the Syncarida. Journ. Linn. Soc. London, Zool., vol. 37, pp. 467-472, 9 figs.

1934. On the embryology of the crustacean *Nebalia bipes*. Philos. Trans. R. Soc. London, ser. B, vol. 223, pp. 163-238, 17 text figs., pls. 20-28.

MARCUS, E.

1929. Zur Embryologie der Tardigraden. Zool. Jahrb., Anat., vol. 50, pp. 333-384, 31 text figs., pl. 8.

MELLANBY, HELEN

1936. The later embryology of *Rhodnius prolixus*. *Quart. Journ. Micr. Sci.*, vol. 79, pp. 1-42, 22 text figs.

METSCHNIKOFF, E.

1882. Vergleichend-embryologische Studien. *Zeitschr. wiss. Zool.*, vol. 36, pp. 432-444, pl. 28.

MEYER, A.

1929. Die Entwicklung der Nephridien und Gonoblasten bei *Tubifex rivulorum* Lam. nebst Bemerkungen zum natürlichen System der Oligochäten. *Zeitschr. wiss. Zool.*, vol. 133, pp. 517-562, 31 figs.

MEYER, E.

1887. Studien über den Körperbau der Anneliden. I-III. *Mitt. Zool. Sta. Neapel*, vol. 7, pp. 592-741, pls. 22-27.
1891. Die Abstammung der Anneliden. Der Ausprung der Metamerie und die Bildung des Mesoderms. *Biol. Centralbl.*, vol. 10, pp. 296-308.
1901. Studien über den Körperbau der Anneliden. V. *Mitt. Zool. Sta. Neapel*, vol. 14, pp. 247-385, pls. 12-17.

MICHAELSEN, W.

1928. Oligochaeta. Kükenthal and Krumbach's *Handbuch der Zoologie*, vol. 2, 2d half.

MICHEL, A.

1898. Recherches sur la régénération chez les Annélides. *Bull. Sci. France et Belgique*, vol. 31, pp. 245-417, pls. 13-19.

NEEDHAM, A. E.

1937. Some points in the development of *Neomysis vulgaris*. *Quart. Journ. Micr. Sci.*, vol. 79, pp. 559-588, pls. 23, 24.

NELSON, J. A.

1904. The early development of *Dinophilus*: a study in cell-lineage. *Proc. Acad. Nat. Sci. Philadelphia*, vol. 56, pp. 687-737, pls. 43-48.
1907. The morphology of *Dinophilus conklini* n. sp. *Proc. Acad. Nat. Sci. Philadelphia*, vol. 59, pp. 82-143, pls. 12, 13.
1915. The embryology of the honey bee. *Princeton Univ. Press*.

PACKARD, A. S.

1898. A text-book of entomology. New York.

PATTEN, W., and HAZEN, A. P.

1900. The development of the coxal gland, branchial cartilages, and genital ducts of *Limulus polyphemus*. *Journ. Morph.*, vol. 16, pp. 459-502, pls. 22-28.

PATTEN, W., and REDENBAUGH, W. A.

1900. Studies on *Limulus*. I. The endocrania of *Limulus*, *Apus*, and *Mygale*. *Journ. Morph.*, vol. 16, pp. 1-26, pls. 1, 2.

PENNNERS, A.

1924. Die Entwicklung des Keimstreifs und die Organbildung bei *Tubifex rivulorum* Lam. *Zool. Jarb., Anat.*, vol. 45, pp. 251-308, 32 text figs., pls. 12-14.
1930. Entwicklungsgeschichtliche Untersuchungen an marinen Oligochäten. II. Furchung, Keimstreif und Keimbahn von *Pachydriulus (Lumbri-cillus) lineatus* Müll. *Zeitschr. wiss. Zool.*, vol. 137, pp. 55-119, 40 figs.

PENNERS, A., and STÄBLEIN, A.

1930. Über die Urkeimzellen bei Tubificiden (*Tubifex rivulorum* Lam. und *Limnodrilus udekemianus* Claparède). Zeitschr. wiss. Zool., vol. 137, pp. 606-626, 13 figs.

PETRUNKEVITCH, A.

1922. The circulatory system and segmentation in Arachnida. Journ. Morph., vol. 36, pp. 157-188, pls. 1, 2.
1933. An inquiry into the natural classification of spiders, based on a study of their internal anatomy. Trans. Connecticut Acad. Arts Sci., vol. 31, pp. 299-389, 13 pls.

PFLUGFELDER, O.

1932. Über den feineren Bau der Augen freilebender Polychäten. Zeitschr. wiss. Zool., vol. 142, pp. 540-586, 24 figs.
1932 a. Über den Mechanismus der Segmentbildung bei der Embryonalentwicklung und Anamorphose von *Platyrhacus amauros* Attems. Zeitschr. wiss. Zool., vol. 140, pp. 650-723, 40 figs.

PHILIPTSCHENKO, J.

1908. Beiträge zur Kenntnis der Apterygoten. II. Über die Kopfdrüsen der Thysanuren. Zeitschr. wiss. Zool., vol. 91, pp. 93-111, pls. 5, 6.

POKROWSKY, S.

1899. Noch ein Paar Kopfhöcker bei den Spinnenembryonen. Zool. Anz., vol. 22, pp. 272-273, 1 fig.

POMPECKJ, J. F.

1927. Ein neues Zeugnis uralten Lebens. Paläontol. Zeitschr., vol. 9, pp. 287-313, pl. 5.

RABL, C.

1879. Über die Entwicklung der Tellerschnecke. Morph. Jahrb., vol. 5, pp. 562-660, pls. 32-38.
1889. Theorie des Mesoderms. Morph. Jahrb., vol. 15, pp. 113-252, pls. 7-10.

REYNOLDS, J. M.

1935. A new contribution to the problem of segmentation in the Arthropoda. Amer. Journ. Sci., vol. 30, pp. 373-382.

ROBINSON, MARGARET

1907. On the segmentation of the head of Diplopoda. Quart. Journ. Micr. Sci., vol. 51, pp. 607-624, pl. 37.

ROONWAL, M. L.

1937. Studies on the embryology of the African migratory locust, *Locusta migratoria migratorioides* Reiche and Frm. II. Organogeny. Philos. Trans. R. Soc. London, ser. B, vol. 227, pp. 175-244, pls. 1-7.

RUSER, MAGDALENE

1933. Beiträge zur Kenntnis des Chitins und der Muskulatur des Zicken (*Ixodidae*). Zeitschr. Morph. Ökol. Tiere., vol. 27, pp. 199-261, 39 figs.

SCHIMKEWITSCH, W.

1895. Über Bau und Entwicklung des Endosternits der Arachniden. Zool. Jahrb., Anat., vol. 8, pp. 191-216, pls. 10, 11.
1906. Über die Entwicklung von *Thelyphonus caudatus* (L.), vergleichen mit derjenigen einiger anderer Arachniden. Zeitschr. wiss. Zool., vol. 81, pp. 1-95, pls. 1-8.

SCHLIEPER, C.

1925. Zur Systematik der Gattung *Nerilla*. Zool. Anz., vol. 62, pp. 229-234, 4 figs.

SCHNEIDER, K. C.

1902. Lehrbuch der vergleichenden Histologie. Jena.

SCHULZE, P.

1936. Trilobita, Xiphosura, Acarina. Eine morphologische Untersuchungen über Plangleichheit zwischen Trilobiten und Spinnentieren. Zeitschr. Morph. Ökol. Tiere, vol. 32, pp. 181-226, 39 figs.
1938. Über rein glabellare Karapaxbildungen bei Milben und über die Umgestaltung des Vorderkörpers der Ixodidea als Folge der Gnathosomaentstehung. Zeitschr. Morph. Ökol. Tiere, vol. 34, pp. 135-149, 18 figs.

SCLATER, W. L.

1888. On the early stages of the development of a South American species of *Peripatus*. Quart. Journ. Micr. Sci., vol. 28, pp. 343-363, pl. 24.

SEDGWICK, A.

1884. On the origin of metameric segmentation and some other morphological questions. Quart. Journ. Micr. Sci., vol. 24, pp. 43-82, pls. 2, 3.
1885. The development of *Peripatus capensis*. Part I. Quart. Journ. Micr. Sci., vol. 25, pp. 449-468, pls. 31, 32.
1886. The development of the cape species of *Peripatus*. Part II. Segmentation of the ovum and formation of the layers. Quart. Journ. Micr. Sci., vol. 26, pp. 175-212, pls. 12-14.
1887. The development of the cape species of *Peripatus*. Part III. The changes from stage A to stage F. Quart. Journ. Micr. Sci., vol. 27, pp. 467-550, pls. 34-37.
1888. The development of the cape species of *Peripatus*. Part IV. The changes from stage G to birth. Quart. Journ. Micr. Sci., vol. 28, pp. 373-396, pls. 26-29.

SHEARER, C.

1912. The problem of sex determination in *Dinophilus gyrotilatus*. Quart. Journ. Micr. Sci., vol. 57, pp. 329-371, pls. 30-34.

SHELDON, LILIAN

- 1888, 1889. On the development of *Peripatus Novae-Zelandiae*. Quart. Journ. Micr. Sci., vol. 28, pp. 205-237, pls. 12-16; vol. 29, pp. 283-293, pls. 25, 26.

SILVESTRI, F.

1933. Sulle appendici del capo degli "Japygidae" (*Thysanura entotropha*) e rispettivo confronto con quelle dei Chilopodi, dei Diplopodi e dei Crostacei. 5th Congr. Internat. Entom., Paris, 1932, pp. 329-343, 7 figs.

SNODGRASS, R. E.

1933. Morphology of the insect abdomen. Part II. The genital ducts and the ovipositor. Smithsonian Misc. Coll., vol. 89, no. 8, 148 pp., 58 figs.
1936. Morphology of the insect abdomen. Part III. The male genitalia. (Including arthropods other than insects). Smithsonian Misc. Coll., vol. 95, no. 14, 96 pp., 29 figs.

SOKOLOW, I.

1911. Über eine neue *Ctenodrilus*art und ihre Vermehrung. Zeitschr. wiss. Zool., vol. 97, pp. 547-603, pls. 27-29.

SOLLAUD, E.

1923. Recherches sur l'embryogénie des Crustacés décapodes de la sous-famille des "Palemoninae." Bull. Biol. France et Belgique, Suppl., vol. 5, 234 pp., 5 pls.
1933. Le blastopore et la question du "prostomium" chez les Crustacés. Assoc. Française Avanc. Sci., 57th Sess., Chambéry, pp. 321-327, 2 figs.

STAFF, F.

1910. Organogenetische Untersuchungen über *Criodrilus lacuum* (Hoffmstr.). Arb. zool. Inst. Wien, vol. 18, pp. 227-256, 2 pls.

STEPHENSON, J.

1930. The *Oligochaeta*. Oxford.

STORCH, O.

1912. Zur vergleichenden Anatomie der Polychäten. Verhandl. zool.-botan. Ges. Wien, vol. 62, pp. 81-97, 4 figs.
1913. Vergleichend-anatomische Polychätenstudien. Sitzungsab. Akad. wiss. Wien, Math.-natur. Kl., vol. 122, Ab. 1, pp. 877-988, 3 pls.

STUMMER-TRAUNFELS, v. R. R.

1903. Beiträge zur Anatomie und Histologie der Myzostomen. I. *Myzostoma asteriae* Marenz. Zeitschr. wiss. Zool., vol. 75, pp. 495-595, pls. 34-38.

SURFACE, F. M.

1907. The early development of a polyclad *Planocera inquilina* Wh. Proc. Acad. Nat. Sci. Philadelphia, vol. 59, pp. 514-559, pls. 35-40.

TANNREUTHIER, G. W.

1915. The embryology of *Bdellodrilus philadelphicus*. Journ. Morph., vol. 26, pp. 143-216, 26 text figs., 8 pls.

TILLYARD, R. J.

1930. The evolution of the class Insecta. Roy. Soc. Tasmania, Papers and Proc., 1930, 89 pp., 19 figs.
1932. The evolution of the class Insecta. Amer. Journ. Sci., vol. 23, pp. 529-539.
1935. Evolution of progoneate and opisthogoneate types in the myriapod-hexapod group of terrestrial Arthropoda. Amer. Journ. Sci., vol. 30, pp. 438-449.

TORREY, J. C.

1903. The early embryology of *Thalassema mellita* (Conn.) Ann. New York Acad. Sci., vol. 14, pp. 165-246, 2 pls.

TREADWELL, A. L.

1901. The cytogeny of *Podarke obscura* Verrill. Journ. Morph., vol. 17, pp. 399-486, pls. 36-40.

VERSLUYS, J., and DEMOLL, R.

1920. Die Verwandtschaft der Merostomata mit den Arachnida und den anderen Abteilungen der Arthropoda. Proc. K. Akad. Wetens. Amsterdam, vol. 23, pp. 739-765.
1923. Das *Limulus*-Problem. Die Verwandtschaftsbeziehungen der Merostomen u. Arachnoideen unter sich u. mit anderen Arthropoden. Ergebnisse u. Fortschritte der Zoologie, vol. 5, pp. 67-388, 123 figs.

VOGT, W.

1935. Die Entwicklung der Antennendrüse der Mysideen. *Zeitschr. Morph. Ökol. Tiere.*, vol. 29, pp. 481-506, 20 figs.

WALCOTT, C. D.

1908. Mount Stephen rocks and fossils. *Canadian Alpine Journ.*, vol. 1, no. 2, pp. 232-248, 4 pls.
 1910. Olenellus and other genera of the Mesonacidae. *Smithsonian Misc. Coll.*, vol. 53, no. 6, pp. 231-422, 22 pls.
 1911. Cambrian geology and paleontology. II. No. 5. Middle Cambrian annelids. *Smithsonian Misc. Coll.*, vol. 57, no. 5, pp. 110-144, pls. 18-23.
 1916. Cambrian geology and paleontology. III. No. 5, Cambrian trilobites. *Smithsonian Misc. Coll.*, vol. 64, no. 5, pp. 303-456, pls. 45-67.
 1931. Addenda to descriptions of Burgess shale fossils. *Smithsonian Misc. Coll.*, vol. 85, no. 3, 46 pp., 23 pls.

WARBURG, ELSA.

1925. The trilobites of the Leptaena limestone in Dalarne. *Bull. Geol. Inst. Univ. Uppsala*, vol. 17, pp. 1-450, 11 pls.

WHITMAN, C. O.

1886. The germ-layers of Clepsine. *Zool. Anz.*, vol. 9, pp. 171-176, 1 fig.

WIESMANN, R.

1926. Zur Kenntnis der Anatomie und Entwicklungsgeschichte der Stabheuschrecke *Carausius morosus* Br. III. Entwicklung und Organogenese der Cölombläsen, 206 pp., 86 figs. *Zool.-vergl. anat. Inst. Univ. Zürich*.

WILSON, E. B.

1889. The embryology of the earthworm. *Journ. Morph.*, vol. 3, pp. 387-462, pls. 16-22.

WOLTERECK, R.

1905. Wurm "kopf," Wurmrumpf und Trochophora. Bemerkungen zur Entwicklung und Ableitung der Anneliden. *Zool. Anz.*, vol. 28, pp. 273-322, 24 figs.

ZACHER, F.

1933. Onychophora. Kükenthal and Krumbach's *Handbuch der Zoologie*, vol. 3, 2d half, pp. 79-138, figs. 57-122.

ZIEGLER, E.

1898. Über den derzeitigen Stand der Cölomfrage. *Verh. Deutschen Zool. Ges.*, 8th Jahresvers., pp. 14-78, 15 figs.

ZILCH, A.

1936. Zur Frage des Flimmerepithels bei Arthropoden. *Zeitschr. wiss. Zool.*, vol. 148, pp. 89-132, 11 figs.





SMITHSONIAN MISCELLANEOUS COLLECTIONS

VOLUME 97, NUMBER 7

THE DIRECT-HISTORICAL APPROACH IN PAWNEE ARCHEOLOGY

(WITH SIX PLATES)

BY

WALDO R. WEDEL

Assistant Curator of Archeology
U. S. National Museum



(PUBLICATION 3484)

CITY OF WASHINGTON

PUBLISHED BY THE SMITHSONIAN INSTITUTION

OCTOBER 19, 1938

SMITHSONIAN MISCELLANEOUS COLLECTIONS
VOLUME 97, NUMBER 7

THE DIRECT-HISTORICAL APPROACH IN PAWNEE ARCHEOLOGY

(WITH SIX PLATES)

BY
WALDO R. WEDEL
Assistant Curator of Archeology
U. S. National Museum



(PUBLICATION 3484)

CITY OF WASHINGTON
PUBLISHED BY THE SMITHSONIAN INSTITUTION
OCTOBER 19, ⁴/₁ 1938

The Lord Baltimore Press
BALTIMORE, MD., U. S. A.

THE DIRECT-HISTORICAL APPROACH IN PAWNEE ARCHEOLOGY

By WALDO R. WEDEL

Assistant Curator of Archeology, U. S. National Museum

(WITH SIX PLATES)

When the University of Nebraska Archeological Survey was established in 1929, its then director, Dr. W. D. Strong, envisaged two primary objectives. The first was a preliminary survey of the State, including both surface reconnaissance and sampling excavations, designed to give a general bird's-eye view of the area as a whole. With this was combined a second aim, namely, an effort to locate and work such sites as could be definitely identified with villages visited and recorded by the early white explorers in eastern Nebraska. It was believed that by isolating and clearly defining the archeological characteristics of the historic peoples a whole series of sites could soon be removed from the category of unknowns; and furthermore, that a comparison of materials so identified with earlier remains in the region might open lines of attack which would permit the establishing of a time sequence extending "from the known historic into the unknown prehistoric." Toward this second objective a serious beginning had already been made by A. T. Hill, of Hastings, Nebr., who since 1922 had accumulated a considerable quantity of archeological materials from sites identified as Pawnee through critical study of early nineteenth century maps and narratives. This collection, as well as numerous valuable historical leads, was promptly made available to Dr. Strong and his coworkers, and it became the starting point for the study of Pawnee archeology. In this paper it is proposed to review very briefly the methods and some results of this approach to prehistory in the Pawnee area.

It was not chance alone that prompted selection of the Pawnee for the first systematic attempt at isolating a historic archeological complex in Nebraska. Aside from Hill's pioneer labors, consideration was given to the fact that this tribe was one of the largest, best known, and most powerful in the entire Plains area. Among the semi-sedentary so-called village tribes of the Missouri valley, including both Caddoan and Siouan groups, probably none shows evidence

for a longer occupancy of its historic locale than the Pawnee. Furthermore, of all the Nebraska peoples, the Pawnee appear to have offered the most effective and prolonged resistance to the host of alien practices introduced by the whites and to have retained longest their own customs. As to documentation, allusions to the Pawnee may be found from almost the very beginnings of recorded European penetration into the interior United States, although it is true that many of the seventeenth and early eighteenth century sources of information leave much to be desired. Prior to about 1800, hazy geographical concepts, occasional tribal shiftings, and the often hearsay origin of the explorer's observations made impossible the recording of village locations with the exactness necessary to permit their individual identification today. After that date, thanks to the lucid narratives and excellent maps of such men as Dulac, Pike, Lewis and Clark, Long, and others, the historical record has enabled us to correlate with reasonable certainty the native towns with known archeological sites. Excavations in sites so identified have revealed the distinguishing characteristics of historic Pawnee culture, insofar as these include nonperishable material traits. As the term is now used in Nebraska prehistory and in this paper, historic Pawnee archeology refers to the antiquities from documented village sites where the Pawnee are known to have been living in or after circa 1800.¹ Needless to say, throughout this period the archeological picture can be greatly enriched through the ethnographic observations of many of the white travelers.

During the nineteenth century, the Pawnee villages with but two or three apparent exceptions were centered about the confluence of the Loup with the Platte River. Both of these streams flow in a general easterly direction through broad flat-floored valleys inclosed on either side by lofty bluffs. Above the mouth of Shell Creek the native towns stood on terraces or second bottoms well out of reach of floods; below this point suitable terraces are mostly lacking and the sites are situated on the bluffs with the river sweeping past their bases. The tree-fringed watercourses are in marked contrast to the dry rolling, formerly grass-covered, uplands which lie beyond the valley margins. To the natives the latter were suited only for hunting and it was the fertile river bottoms, with an abundance of wood, water, arable ground, and shelter, that determined the location of their villages.

¹ For a discussion of historic Pawnee archeological remains see Wedel, 1936, and Strong, 1935, pp. 55-61.

The extreme limits of the known Pawnee settlements were, to the west, near St. Paul on the Loup and Central City on the Platte; to the east, downriver, they ran to Leshara or Yutan on the Platte (see fig. 1 for location of all sites discussed herein). Within this 120-mile stretch of river valley they shifted back and forth as fancy or circumstance dictated, leaving it only for their seasonal hunting excursions. The exceptions, it may be noted, included two sites on the Republican near the Kansas-Nebraska line and one on the Blue near Blue Springs, Nebr. That this nineteenth century restriction of habitat was in effect long before will become apparent presently when certain additional historical and ethnographic facts are considered. Here it is desired to add only the observation that all of these village sites, in addition to a somewhat decadent aboriginal material culture, yield also many articles of iron, copper, brass, and glassware.

Within this same area, but of even more limited distribution, are found other sites whereon the native remains are far more abundant, of superior quality, and associated with much smaller quantities of white contact material. These sites extend along the Platte-Loup riverway from Schuyler on the east to the vicinity of Genoa on the west, a distance of approximately 50 miles; they are mostly on the north bank, but one is also known on the south side. Generally, the sites are large (from 15 to 100 acres or more) and compactly arranged; not infrequently they seem to have been located on bluffs or hilltops with an eye to defensibility and in a few instances they were further protected by earth walls and ditches. To date about a dozen have been placed on record. The sites are particularly abundant from Monroe westward, where for more than 8 miles remains occur almost continuously along the Loup and on the lower portion of Beaver Creek. In the aggregate these antiquities cover many hundreds of acres, and prior to introduction of modern farming operations, innumerable house circles, middens, and artifacts were to be found. Because of their occurrence in the very heart of the historic Pawnee habitat and since they yielded smaller amounts of contact material than the identified nineteenth century Pawnee sites while exhibiting many similarities to the latter, it was thought that they might prove to be an earlier, if still post-European, phase of Pawnee culture. Consequently, in 1931, as a sequel to the study of the historic Pawnee, two of these protohistoric² sites were partially

² Protohistoric sites yield limited amounts of glass and metal trade wares, indicating their occupancy, at least in part, since the arrival of Europeans. They

examined by parties from the University of Nebraska. About 8 weeks were devoted to excavation of houses and middens at the Burkett site near Genoa and at the Gray-Wolfe site north of Schuyler. All but one week of this field-work was in direct charge of the present writer, under the supervision of Dr. Strong and with much active assistance in the field from Mr. Hill. A detailed description of the findings has been published recently by the University, and the remains have been assigned to the "Lower Loup Focus of an unnamed aspect of the Upper Mississippi Phase."³ A wealth of additional information has since been gathered by Mr. Hill for the Nebraska Historical Society at three other protohistoric sites near Genoa. This latest work, completed in 1936 and as yet unpublished, included the opening of 10 houses, a number of large and prolific caches, and the collecting of several thousand artifacts, all at sites lying within 4 or 5 miles of the Burkett site. Pending future analysis and detailed comparison, it must suffice to say that preliminary examinations indicate a close similarity between this material and that already described in print from the Burkett and Gray-Wolfe sites. In passing it may be noted also that extensive surface collections from most of the other protohistoric sites in the immediate locality diverge in no significant respect. In short, a fairly uniform and consistent cultural complex seems to be manifested at the sites designated on the map as belonging to the Lower Loup Focus.

Historic archeology in Nebraska received added stimulus in the summer of 1935, when Hill explored the large protohistoric Leary site on the Nemaha River in the extreme southeastern corner of the State. This has been elsewhere described and identified as Oneota. Midwestern archeologists are inclined to view the Oneota culture in Iowa and adjacent States as possibly early Siouan.⁴ There are indications that the Leary site was inhabited contemporaneously with or possibly slightly earlier than the known sites of the Lower Loup

differ from historic sites in that the written records are too general to permit their individual identification with villages actually visited by white men. In time they antedate 1800.

³ Dunlevy, 1936, pp. 147-248 (quot. p. 216). A discussion of the placing of the Lower Loup Focus in the McKern taxonomic system is beyond the scope of this paper. However, it may be pointed out that at least four of the nine Upper Mississippi Phase determinants listed by Deuel (F. C. Cole and T. Deuel, *Rediscovering Illinois*, table 2, p. 214, 1936) are unreported from the Lower Loup Focus and incidentally from the historic Pawnee as well. The present writer regards as debatable the assignment of either complex, or of a hypothetical aspect which might include both, to the Upper Mississippi Phase.

⁴ Hill and Wedel, 1936; Griffin, 1937.

Focus but no documentary record exists as to the tribe which inhabited it. It definitely antedates the historic Pawnee sites of the nineteenth century. This is of some interest because there are Pawnee traditions pointing to early residence of the tribe somewhere in this section of southeastern Nebraska, suggesting the possibility of a generic connection with the Oneota.

As regards the relation of these three postcontact archeological complexes to one another, dissimilar conclusions have been reached by different field and laboratory workers. Strong expressed the belief that the sites now labeled collectively as the Lower Loup Focus probably represented a very early historic horizon directly ancestral to the somewhat simpler and decadent Pawnee culture of the nineteenth century. His use of the term "protohistoric Pawnee" in speaking of these remains reflects a view with which the present writer has elsewhere indicated his general agreement.⁵ Dunlevy, on the other hand, dissenting after her detailed analysis of material from two of these sites, was persuaded that the Lower Loup Focus is more closely related to the Oneota than to the historic Pawnee.⁶ Since these differences of viewpoint occur among individuals dealing with substantially the same materials, it seems worthwhile to re-examine the data on which they rest.

In the accompanying table the presence or apparent absence of traits has been indicated for each of the three cultural complexes above mentioned. The traits, totaling 120, have been grouped in seven categories which, with exception of ceramics and miscellaneous items, are based upon function rather than on form or substance. Traits for the historic Pawnee and the Lower Loup Focus have been compiled largely but not exclusively from published sources. In the absence of complete analyses for the recently worked sites, the data therefrom have been incorporated in and added to a check list based on the published studies. Actually, this somewhat superficial treatment involved no changes in the list other than its slight expansion to include a larger number of traits. Data on the Oneota Aspect, including three Wisconsin variants or foci, have been drawn from a list furnished by W. C. McKern, of the Milwaukee Public Museum, which has been supplemented by the published report on the Leary site in Nebraska. No attempt has been made to weight the various elements or to determine the degree to which a particular trait may be present in one or another of the groups. It has not always been

⁵ Strong, *op. cit.*, pp. 68, 297; Wedel, *op. cit.*, pp. 38-42, 74.

⁶ Dunlevy, *op. cit.*, p. 216.

possible to refine the traits as fully as desired, owing to differences in terminology in the sources used and to inability to examine all the material at first hand. It is believed, however, that the data are sufficiently extensive and representative to be strongly indicative of trends, at least.

TABLE I.—*Presence or Absence of Traits in the Historic Pawnee, the Lower Loup Focus, and the Oneota Aspect*

	A Historic Pawnee	B Lower Loup Focus	C Oneota Aspect
I. ARCHITECTURE AND VILLAGE COMPLEX			
Villages			
1. Large, intensively occupied sites.....	x	x	x
2. Walled or defensively located.....	x	x	
3. Numerous outside caches.....			x
Houses			
4. Shallow semisubterranean circular earth-covered...	x	x	
5. Vestibule entrance in east or south.....	x	x	
6. Unlined central firepit.....	x	x	
7. Bison-skull shrine opposite door.....	x	x	
8. Four main central posts.....	x	x	
9. More than four central posts.....	x	x	
10. One or two rows of widely spaced outer posts.....	x	x	
11. Inside caches	x	x	
12. Numerous small, closely set, slanting wall posts.....	x	x	
II. CERAMIC COMPLEX			
Temper			
13. Grit	x	x	
14. Shell		x	x
Texture			
15. Fine to medium coarse.....	x	x	x
Structure			
16. Flaky	x	x	x
17. Granular	x		
Hardness			
18. 1-4, softer predominating.....			x
19. 3-6, 4-5 predominating.....	x	x	
Surface finish			
20. Irregularly smoothed	x	x	x
21. Polished (imperfectly)	x	x	x
22. Marked by grooved paddle.....	x	x	
Color			
23. Light to dark gray and buff, dull terra cotta.....	x	x	x
Thickness			
24. $\frac{3}{8}$ - $\frac{1}{2}$ inch range.....	x	x	x
Lip form			
25. Squared	x	x	x
26. Rounded	x	x	x

TABLE 1.—*Presence or Absence of Traits in the Historic Pawnee, the Lower Loup Focus, and the Oneota Aspect* (continued)

	A Historic Pawnee	B Lower Loup Focus	C Oneota Aspect
Rim form			
27. Plain high direct flaring.....	x	x	x
28. Collar or braced.....	x	x	
29. Cloistered		x	
Neck form			
30. Line of juncture between rim and body.....	x	x	x
31. More pronounced	x	x	
Orifice			
32. Broad	x	x	x
33. Round	x	x	x
34. Oval		x	x
Shoulder form			
35. Round	x	x	x
Basal form			
36. Rounding	x	x	x
37. Subconical	x	x	
Handles			
38. Narrow to broad, flat, straplike, paired.....		x	x
39. Loop		x	x
40. Alternate collar tabs form handles.....	x		
41. Multiple	x	x	
Decoration			
42. Lip	x	x	x
43. Shoulder area to lip, neck plain.....	x	x	x
44. Incised rectilinear parallel line motifs.....	x	x	x
45. Opposed series of parallel lines.....	x	x	x
46. Herringbone and chevron on rim.....	x	x	
47. Concentric pendent chevrons inside rim.....			x
48. Concentric circle motif and/or cross.....			x
49. Geometric series of lines and dots.....			x
50. Trailed or fluted decoration.....			x
Miscellaneous			
51. Small bowls	x	x	
52. Small decorated "fishtail" figurines.....	x	x	
53. Use of red wash or pseudo-slip.....	x	x	
54. Perforated pottery disks.....		x	x
55. Pot lids with handles.....	x		
56. Cut sherds and bisected vessels.....			x
III. HORTICULTURE AND FOOD-GATHERING			
57. Intensive horticulture, with maize, beans, etc.....	x	x	x
58. Hoes made of bison scapulae.....	x	x	x
59. Wooden mortar	x		
60. Stone mortar: irregular, shaped, flattened surface...	x	x	x

TABLE 1.—*Presence or Absence of Traits in the Historic Pawnee, the Lower Loup Focus, and the Oneota Aspect (continued)*

	A Historic Pawnee	B Lower Loup Focus	C Oneota Aspect
IV. MILITARY AND HUNTING COMPLEX			
61. Arrowpoints, small triangular unnotched.....	x	x	x
62. Knives: diamond-shaped, beveled.....		x	x
63. Knives: oval and/or flake.....	x	x	x
64. Scrapers: small to medium planoconvex.....	x	x	x
65. Scrapers: large elliptical quartzite or sandstone....	x	x	
66. Drills	x	x	x
67. Abraders: paired longitudinally grooved sandstone..	x	x	x
68. Abraders: amorphous pumice lumps.....			x
69. Mauls: grooved	x	x	x
70. Axes: grooved	?		x ^a
71. Celts: polished diorite or hematite.....	x		x
72. Hammerstones, pitted	x	x	
73. Adz-shaped elkhorn hide scrapers.....			x
74. Deerhorn "cylinders" or tapping tools.....			x
75. Deerhorn tip flakers.....		x	x
76. Deerhorn projectile points, conical, socketed.....			x
77. Bone projectile points, socketed, square or conical...		x	
78. Bone projectile points, stemmed.....		x	
79. Bundles of cane (arrowshafts?).....		x	
80. Perforated ribs (arrowshaft straighteners).....	x	x	x
81. Notched fleshing tools or grainers.....	x	x	
82. Shoulder blade scrapers.....			x
83. Celtlike antler scrapers.....			x
84. Metapodial beamers			x
85. Bone fishhooks			x
V. DRESS, TEXTILES, AND ADORNMENT			
86. Bison-hair cloth and/or cordage.....	x		x
87. Awls	x	x	x
88. Eyeleted needles			x
89. Plume holder	x		
90. Roach spreader	x		
91. Combs		x	
92. Bracelets and/or gorgets.....	x	x	x
93. Paint bones ("brushes").....	x	x	
94. Polished bone tubes.....	x	x	x
95. Rush matting	x		
96. Flat polished-bone mat needles.....			x
97. Twined bags of vegetal material.....		x	
98. Shell ornaments, variously shaped.....	x	x	x
VI. CEREMONIAL COMPLEX			
99. Primary extended burials.....			x
100. Primary flexed burials.....	x	x	x
101. Secondary bundle burials.....			x ^a

^a Rare, probably atypical.

TABLE I.—*Presence or Absence of Traits in the Historic Pawnee, the Lower Loup Focus, and the Oneota Aspect (continued)*

	A Historic Pawnee	B Lower Loup Focus	C Oneota Aspect
VI. CEREMONIAL COMPLEX— <i>Continued</i>			
102. Grave furniture	x		x
103. Burial in dug pits or caches.....	x	x	x
104. Burial in or under mounds.....			x
105. Gaming stones ?; bun-shaped, flat pitted face.....			x
106. Gypsum crystals, worked.....		x	
107. Shaped balls of crystalline stone (grave finds).....	x		
108. "Whetstones" (grave finds).....	x		
109. Pipes of polished stone.....	x	x	x
110. Pipes of clay.....		x	
111. Pipes: elbow-shaped or equal-armed.....	x	x	x
112. Pipes: "Siouan" type, stem projects beyond bowl....	x		
113. Pipes: disk bowl.....		x	x
114. Pipes: "Micmac"	x		
115. Orna mented animal skulls.....	x	x	
VII. MISCELLANEOUS			
116. Incised stone tablets.....	x	x	x
117. Bison horn spoons.....	x		
118. Tanged mussel shell spoons.....			x
119. Ulua "picks"	x	x	x
120. Tally bones (scored ribs).....		x	x
	80	82	74

ANALYSIS OF TABLE: SUMMARY

Total number of traits—120

Historic Pawnee has 80, or 66.6 percent of total

Lower Loup Focus has 82, or 68.3 percent of total

Oneota Aspect has 74, or 61.6 percent of total

"Universal" traits—39, or 32.5 percent of total

39 universals in 80 historic Pawnee elements..... 48.8 percent

39 universals in 82 Lower Loup Focus elements..... 47.6 percent

39 universals in 74 Oneota Aspect elements..... 52.7 percent

Out of total of 120 traits—

26 occur only in historic Pawnee and Lower Loup Focus..... 21.7 percent

9 occur only in Lower Loup Focus and Oneota Aspect..... 7.5 percent

3 occur only in historic Pawnee and Oneota Aspect..... 2.5 percent

On basis of 81 nonuniversal traits these percentages become
respectively 32, 11, and 3.7.

Traits occurring in only one complex—

Historic Pawnee 12

Lower Loup Focus..... 8

Oneota Aspect 23

Analysis of the table shows first that out of the total of 120 different elements the historic Pawnee and the Lower Loup Focus have, respectively, 80 and 82 (66.6 and 68.3 percent), and the Oneota Aspect has 74 (or 61.6 percent). Of the 120 traits, furthermore, 39 are common to all three culture complexes. Since this represents, respectively, 48.8, 47.6, and 52.7 percent of those found in each complex, it is evident that there is a strong underlying relationship. These "universals" include elements in practically all of the categories, but occur least commonly under the "Architecture and Villages" heading.⁷ As regards specific relationships between any two of the three complexes, we find that 26 traits, or 21.7 percent, occur only in historic Pawnee and the Lower Loup Focus;⁸ 9, or approximately 7.5 percent, only in the Lower Loup Focus and the Oneota;⁹ and 3, or 2.5 percent, only in historic Pawnee and Oneota. Since it is these relationships within the defined universe of three which are the principal concern here, we may reduce our totals and sharpen the above differentiations by omitting the "universal" traits. Thus, using the 81 nonuniversals as our basis, the percentages become, respectively, 32, 11, and 3.7. Whichever set of figures is taken, it is apparent that the table indicates very nearly three times as many traits in common between the historic Pawnee and the Lower Loup Focus (and in no other) as in the Lower Loup Focus and the Oneota.¹⁰ Evidently the suggested connection between the first two complexes, considered on purely archeological grounds alone, is considerably closer than that between the second pair. This is the more striking in view of the previously indicated fact that the Lower Loup Focus flourished at the very beginning of European contact and approximately con-

⁷ The single rectangular earthlodge floor found at the Leary site has not been included in the present table since there seems to be general agreement among field workers that this type of structure is not characteristic of the Oneota. I am inclined to agree with McKern's suggestion that the occurrence of earthlodges in the western Oneota sites "may be due to the taking on of foreign traits after leaving the area of earlier occupation." (Letter of Oct. 28, 1937.)

⁸ Including among others nine in architecture, besides such elements as decided predominance of grit tempering, use of grooved paddle in surfacing pottery, small decorated "fishtail" figurines of clay, large elliptical quartzite hide scrapers, bone paint "brushes," notched fleshers, ornamented animal skulls (rare), etc. In the trait list these are Nos. 2, 4-13, 19, 22, 28, 31, 37, 41, 46, 51-53, 65, 72, 81, 93, 115.

⁹ Including five in ceramics, besides diamond-shaped beveled knives, platform disk pipes, scored ribs (tallies?), and antler tip flakers, Nos. 14, 34, 38, 39, 54, 62, 75, 113, 120.

¹⁰ Cf. Dunlevy, *op. cit.*, p. 216.

temporaneously with the Oneota, whereas the Pawnee traits are based on sites inhabited one or more centuries later toward the close of the tribe's residence in Nebraska. The conclusion seems inescapable that the Lower Loup Focus stands in very much closer and more direct relationship genetically to the later historic Pawnee than to the contemporaneous Oneota peoples.¹¹

With the Oneota culture and its probable Siouan connections we shall not further concern ourselves here. Its rôle in the development of later native civilization west of the Missouri is not yet clear, although it probably introduced into the Pawnee area various innovations in ceramics, pipe-making, stone-working, and certain other fields of activity. At the moment, there is no reason to regard it as in any sense basic to historic Pawnee culture, since its contributions seem to have been rather in matters of detail.

Bearing directly on the question of the nineteenth century Pawnee and their postulated descent from the Lower Loup Focus are certain noteworthy nonarcheological considerations. These seem to have been generally overlooked by those who challenge such a correlation on grounds (1) that the Pawnee have no legends concerning the sites, and (2) that the recent occupancy of the region by that tribe proves nothing as to its connection with the older remains. Both points can be met squarely with recorded data. Thus, to take up the first,

¹¹ The kinds of traits comprising similarities and dissimilarities in the respective pairings is perhaps of as much significance as the absolute numbers. For example, while many of the hunting and skin-dressing practices were similar throughout, important differences are probably implied in the presence of fish-hooks and metapodial (split leg bone type) beamers in the Oneota. Both the latter items are widespread throughout the eastern United States, incidentally occurring also in prehistoric cultures in the Plains. The Pawnee and Lower Loup peoples apparently did not fish, and the outstanding feature of their skin-working industry was its distinctly Plains character; e. g., large elliptical quartzite scrapers, the notched flesher, bone paint "brushes," and probably the adzlike elkhorn hide scraper. At least a part of the subsistence economy of the Oneota, as well as the supposed bark or thatch house type, mound burials, extended use of woven mats, and a number of other items which this group alone of the three possesses, all tend to link them with eastern peoples and stamp them as comparatively recent arrivals west of the Missouri. The Pawnee and Lower Loup Focus peoples, on the other hand, resemble each other closely in virtually every fundamental respect and such common elements among them as the earth-lodge, pottery, horticulture, and other less distinctive items clearly have considerable historic depth in the eastern Plains. Onto this horticultural base they had grafted a hunting complex of western type, differing considerably but evidently well attuned to the peculiarities of the former. The successful integration of the two modes of life, both involving local ingredients, would in itself suggest a considerable period of adjustment *in loco*.

on at least two occasions, Pawnee Indians have claimed certain of the protohistoric sites as the former dwelling places of their tribe. In 1867 Hayden collected a number of potsherds from "a Pawnee village site on Beaver Creek, Nebraska . . . ," some of which were subsequently figured by Holmes.¹² Hayden nowhere records the exact location of his finds, but Hill has since shown that two very large and almost contiguous protohistoric sites occur on the right bank of Beaver Creek a short distance above its mouth, while 2 or 3 miles to the southwest is the Burkett site (fig. 1, nos. 16-18). The ceramic and other remains from the three are very similar, and they were undoubtedly inhabited by the same people and at about the same time. In all probability Hayden's specimens which are of Lower Loup Focus type were picked up on one of these locations. It is, therefore, noteworthy that he says:

No Pawnee Indian now living knows of the time when this village was inhabited. Thirty years ago [i. e., about 1837] an old chief told a missionary that his tribe dwelt there before his birth, but he knew nothing of the use of stone arrowheads, though, he said, his people used them before the production of iron.

When the "production of iron" here began is not known, but the old chief's story tends to imply habitation of the site in question prior to the middle of the eighteenth century. The claim gains support from another tradition recorded by Bruce in his account of the North brothers and their Pawnee scouts.¹³ This is much more explicit and telling. It alludes to a battle which took place long ago between the Pawnees and the Poncas, when 500 of the latter made a treacherous but unsuccessful attack on a Skidi Pawnee village on Shell Creek north of Schuyler. The time of this alleged raid is wholly unknown, but it could not have taken place recently because there is no historic record to indicate that the Skidi, or for that matter any other Pawnee band, dwelt on Shell Creek as late as 1775 or after. Interestingly enough, at the precise locality where the old Skidi village is said to have stood, is the Gray-Wolfe site, one of the first of the Lower Loup Focus to be intensively studied and also one of the two on which the complex as defined is based. (See fig. 1, nos. 24 and 25.) Finally, in a myth explaining the formation of the Skidi federation, Murie locates by streams two of the ancient villages. One of these was on the Elkhorn River, the other on Looking Glass Creek.¹⁴ This, if far less definitive, is still suggestive, since the lower course of the latter is sprinkled with not one but several related protohistoric sites.

¹² Holmes, 1903, pp. 200-201 and pl. 177; Hayden, 1872, pp. 411-412.

¹³ Bruce, 1932, pp. 42-43.

¹⁴ Murie, 1914, p. 554.

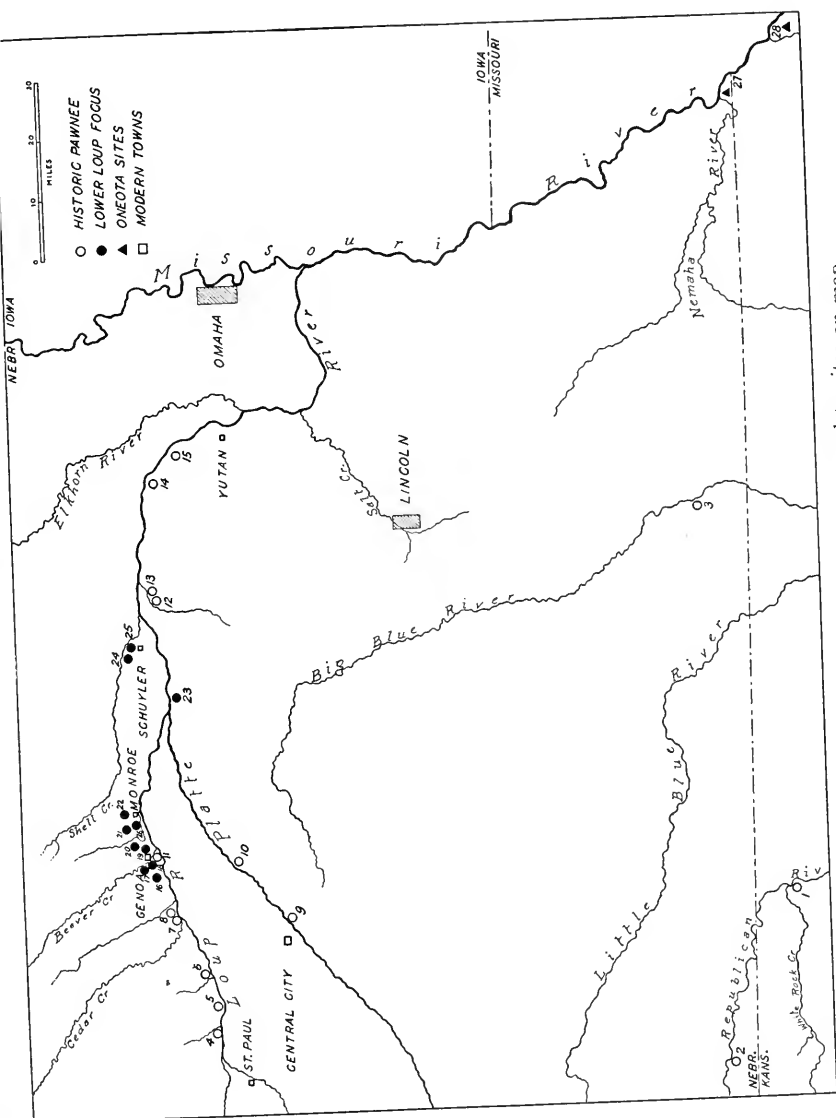


FIG. 1.—List of sites: numbers correspond to sites on map.

Historic Pawnee sites	5. Cottonwood Creek	12-13. Linwood	17. Unbargar	24. Wolfe
1. Kansas Monument	6. Horse Creek	14. McClaine	18. Wright	25. Gray
2. Hill	7. Fullerton	15. Leshara	19. Coffin	26. Foley
3. Blue Springs	8. Plum Creek		20. Larsen	Oneota sites
4. Palmer	9. Hordville	Lower Loup Focus sites	21. Lightner	27. Leary
	10. Clarks	16. Burkett	22. Monroe	28. Fanning
	11. Genoa		23. Bellwood	

Insofar as they are any clue, legends are thus seen to point toward a Pawnee authorship for at least some of the sites.

It is unnecessary to stress the fact that mere areal concurrence of a nineteenth century tribe and a certain archeological complex is, per se, no proof of direct relationship. In the case of the Pawnee this particular argument has never been used except as a possible corroborative circumstance. However, a careful study of the documentary history of the tribe tends to strengthen rather than weaken its force. Here it is possible to pass in review only a few of the more significant points; for further details the reader is referred to recent publications on the Pawnee and citations therein. Prior to the last quarter of the seventeenth century the sources are inconclusive as to the location of the tribe. Coronado, in 1541, places the province of Harahey, tentatively identified as Pawnee territory, north of Quivira. Later Spanish documents locate Quivira somewhere in central Kansas and its people are believed to have been the Wichita. If these identifications are correct, they suggest the presence of the Pawnee in southern or central Nebraska at this early date. A century and a quarter after, in 1666, Perrot mentions the Panys but without defining their habitat.¹⁵ Bandelier notes their presence as captives in New Mexico in the seventeenth century observing that they were not uncommonly ransomed from the Yutes and Apaches.¹⁶ By 1673, however, they had become sufficiently well known to be shown on Marquette's map, as also on that of Hennepin in 1678. Before 1680 the Spanish in New Mexico heard rumors of Frenchmen among the Pawnees, and, wherever the location is given, subsequent narratives consistently place the Pawnee on the Rio Jesus Maria, north of Quivira. This stream is identified by historians with the Platte.¹⁷ For the eighteenth century there are many more records, as well as numerous maps showing ethnic distributions in the Missouri drainage. Curiously enough, with all the unrest and tribal movements manifested therein from time to time, the Pawnee are almost always shown as a relatively stable group localized west of the Missouri on streams identifiable with the Loup, Platte, and possibly Republican Rivers. Particularly interesting in this connection is the 1718 Delisle map of Louisiana and the Mississippi River,¹⁸ because it depicts with remarkable accuracy the geographical details of the present Nebraska region (fig. 2). It shows the Pani (Pawnee) in 12 villages

¹⁵ Wisconsin Hist. Soc., Coll., vol. 16, pp. 15, 27, 1902.

¹⁶ Bandelier, 1890, p. 185, n. 4.

¹⁷ Thomas, 1935, pp. 12, 37.

¹⁸ Delisle, G., *Carte de la Louisiane et du Cours du Mississippi*. Paris, 1718.

first began to reach his area. The discovery of such materials may offer an opportunity to determine approximately the time of occupancy of the sites or levels in which they occurred. Sometimes it is possible to identify beads or other trinkets with types known to have been made at certain stated periods in Europe. There are, of course, limitations to the method, and it must be used with due caution. Such objects as glass beads, copper bells or ornaments, and other small trinkets may have, and probably very often did, spread from village to village and from tribe to tribe, wholly independent of the trader after their original acquisition by the natives. They might thus precede the white man by several years. Also it is possible that the earliest traders left no written records, or that such as they may have left were lost or for other reasons remain unknown today. Still, where trade goods occur in small but consistent amounts in several related and neighboring sites, it seems reasonable to believe that a steady and direct, if perhaps limited, traffic had been established, and that historical records may offer valid clues as to the approximate time involved. It is theoretically possible that stray pieces reached the central Plains indirectly from New Mexico through the expeditions of Coronado (1541), Bonilla and Humana (1594), Oñate (1601), and others, or as a result of raids against the Spanish settlements or their Apache and puebloan proteges. These, however, must have been of minor consequence. As a matter of fact, the Spaniards credit the rival French from Canada with introducing firearms, metal kettles, axes, and the like to the Pawnee,¹⁹ but it is not certain just how early this trade began. The first Frenchman to penetrate the region west and south of the Great Lakes is generally believed to have been Nicolet, who in 1634 visited the Winnebago and Illinois in what is now southern Wisconsin and northern Illinois.²⁰ Owing to the hostility of the Iroquois and for other reasons, this voyage of exploration was not immediately followed up. It seems extremely doubtful that there was any appreciable commerce with tribes west of the Missouri prior to about 1650. By 1680 the Spanish had reports of French trade goods among the Pawnee on the Platte and in 1706 their Apache allies killed a French couple somewhere in what is now northeastern Colorado. All this leads to the inference that regular trade was established in the central Plains region sometime between 1650 and 1700. It is worth noting that from the first the Spanish records relating to French activities in this area uniformly link with

¹⁹ Thomas, 1935, pp. 12ff.

²⁰ Butterfield, 1881.

them the Pawnee who seem to have been in firm possession of the Platte valley.

Archeological findings leave no room for doubt that some at least of the sites belonging to the Lower Loup Focus were inhabited during a period when commercial intercourse was still comparatively limited in volume. Moreover, the European beads and other materials so far studied from these sites, insofar as they can be dated, appear to be of types used in the Indian trade not prior to the latter seventeenth or eighteenth centuries. Finally, no early contact sites have been found in the region, other than those belonging to this complex, which could possibly be connected with the Pawnee or which can be viewed as the residence of settled Indians in contact with early traders.

The historical background as here reviewed sheds significant light on the contention that the Lower Loup Focus may represent some group other than the Pawnee, not necessarily ancestral or even related to them. In the latest published work on this complex, it is suggested that "possible migration could account for the settling of different peoples in the same locality."²¹ Early in this discussion it was pointed out that the village sites of the Lower Loup Focus, although of comparatively restricted distribution, are both numerous and very large. Moreover, since all those so far excavated have consistently yielded limited quantities of copper, glass beads, and (rarely) iron, it follows that they must have flourished for a time after white influences had penetrated into their locality. Even granting that all were not inhabited simultaneously, they undoubtedly indicate the presence here in protohistoric times of a populous, firmly established, and presumably potent ethnic group. Let us assume for the moment that this group was not ancestral nor even related to the Pawnee. We then have the somewhat difficult situation of a numerous and powerful tribe, resident for many years (witness the innumerable middens, earthlodge sites, etc.) in the very heart of the Pawnee territory, clinging to it until after trade contacts had been established with Europeans (circa 1650 or later), and then emigrating so unobtrusively and so completely that the Pawnee, who must have followed closely on their heels so as to be firmly settled in the region by Delisle's time (1718), retained no tradition of their existence. This would not only do violence to Pawnee traditions linking that group with the protohistoric Lower Loup Focus, but would also require an explanation for the apparent absence of any legends of

²¹ Dunlevy, *op. cit.*, p. 215.

an earlier tribe, unrelated but with very similar culture, whom the Pawnee could reasonably be thought to have displaced since establishment of European contacts. Such a theory, furthermore, would presumably postulate a comparatively late incursion for the Pawnee, which is at variance with the ethnographic indications. Pawnee material culture of the nineteenth century, as has been stated, is pretty clearly a composite based essentially on two distinct and fundamentally divergent economies—one horticultural and sedentary, the other hunting and nomadic. The significant constituents of the former, irrespective of their ultimate origin, are now known to have been well established west of the Missouri in prehistoric times. Those of the latter, in part rooted in the very remote past, were shared with numerous other historic tribes of the Plains and particularly with the western bison hunters. The Pawnee seem to have combined the two in harmonious fashion, and so far as adjustment to environmental and ethnic conditions goes, give no evidence whatever of having been recent arrivals in the Nebraska region.

There are other clues. Dunbar has shown how the placement of villages relative to one another has modified certain linguistic usages in accord with local geography.²² During the later years of their residence in Nebraska there were seldom more than three or four villages—in other words, usually one for each of the four bands. At times two or more bands might occupy a single town, but the Skidi seem always to have remained more or less aloof. Both Murie and Grinnell present evidence supporting the view that subgroups within each of the main bands formerly constituted separate villages.²³ Murie credits the Skidi with 13 of these originally. This interesting observation may partially explain the general tendency of the early explorers to assign, usually from hearsay, as many as a score or more towns to the Pawnee nation. Incidentally, too, it may have archeological implications since the Pawnee locality abounds with small and widely scattered precontact earthlodge villages which appear to have a number of features in common with the later ones. The sudden disappearance of the many small prehistoric villages and the presence of a few very large fortified towns in protohistoric times is an archeological puzzle which still awaits solution. Finally, the mythology of the Pawnee is replete with local Nebraska place names such as the Platte, the Loup, the Republican, Nemaha, and others.²⁴ There are migration legends, to be sure, but none which afford any

²² Dunbar, 1880, p. 251.

²³ Murie, 1914, pp. 549-556; Grinnell, 1893, pp. 231-239.

²⁴ Dorsey, 1906.

proof of recent arrival. Three of the five "sacred places" of the tribe were on the Loup and Platte within 50 miles of their junction; the other two were in southern Nebraska and northern Kansas²⁵; and a number of their myths and tales relate directly to this neighborhood.

It must be apparent by this time that there exists little else than academic grounds for questioning the presence of the Pawnee as a firmly ensconced tribe in the Platte-Loup region since at least the coming of the whites. The data of tradition, history, ethnography, and mythology all support this inference. Moreover, the numerous archeological similarities between the historic Pawnee and the earlier Lower Loup Focus reflect essentially the same dual mode of life. Viewed in the light of history, the differences in materials from the two complexes are not so great as to strain the probability of a common authorship. They involve details rather than fundamentals. The greater richness, abundance, and variety of remains on the protohistoric sites indicate a general level of cultural achievement far above that of the historic Pawnee. If, as is very probable, this superiority extends to the nonmaterial side of life as well, then the protohistoric period may be regarded as the climax of social, ceremonial, and political development in the Pawnee area. The culmination must have been reached before 1750. Thereafter came a steady decline which left the nineteenth century peoples in possession of a much simpler and clearly decadent cultural heritage, though the recorded myths as well as many political and ceremonial survivals hark back to the older and better days. Such a regression is perfectly in keeping with the contemporary history of the area: increased pressure from hostile tribes, growing commercial intercourse and territorial quarrels with the whites, new diseases, and a generally more desperate struggle for sheer existence, all of which left scant leisure for cultural advancement.

The leads for future research on this problem are very clear. It is imperative first of all that thorough analyses be made of all available archeological materials from sites of the Lower Loup Focus. These should be carefully compared with similarly detailed studies of collections and data from documented sites of the nineteenth century. Needless to say, identities are not to be expected in all details, since individual, village, and probably band preferences were undoubtedly active factors. The element of time, too, must ever be borne in mind, for over a period of two or three centuries considerable changes are expectable. Another line of attack which has so far been totally

²⁵ Grinnell, *op. cit.*, pp. 358-359.

neglected in this connection is physical anthropology. Skeletal remains either supposedly or certainly attributable to the Pawnee are by no means plentiful, as the early cemeteries remain undiscovered, and the later ones have suffered woefully at the hands of vandals. There is a disturbing possibility that scaffold burial and subsequent dismemberment may have been practised in the early period. Still, careful examination of the material thus far recovered might further illuminate the issue. For obvious reasons, it will probably never be possible to prove empirically that the inhabitants of any one of the Lower Loup Focus sites spoke a Pawnee dialect, since the individual sites cannot be linked with recorded towns. Thus the identification made on other grounds must remain a probability—a very high one, it is true, but still a probability. To maintain from this that the sites are not Pawnee, however, seems a captious argument, particularly in face of the very strong circumstantial evidence in every other respect. On the whole, it may be soundest and perhaps least confusing to retain a nonlinguistic designation for these protohistoric remains, at any rate for the present. For this purpose the term suggested by Dunlevy and used in this paper is as appropriate as any.

SUMMARY AND CONCLUSIONS

In the foregoing pages the relationships between one historic and two protohistoric archeological complexes in Nebraska have been briefly discussed. These are respectively the Pawnee of the nineteenth century, the Lower Loup Focus, and the Oneota Aspect. From the evidence of archeology, history, tradition, mythology, and ethnography, as outlined herein, the following major facts emerge:

(1) Village sites assignable to the Lower Loup Focus, 10 or more in number, occur only in the very heart of the historic Pawnee region about the confluence of the Loup and Platte Rivers.

(2) These sites nearly all yield limited amounts of historical materials, indicating their occupancy at least into very early contact times.

(3) Historic maps and documents show that the Pawnee villages since virtually the earliest contact times were localized in and about this region.

(4) On the basis of available archeological evidence alone, sites of the Lower Loup Focus show a much closer relationship to the later historic Pawnee culture than they do to the contemporaneous Oneota sites.

(5) Pawnee traditions link that tribe directly with several of the protohistoric Lower Loup Focus sites.

(6) Neither history, ethnography, nor recorded traditions offer any proof that another sedentary horticultural tribe inhabited this locality since the arrival of Europeans.

These six points sufficiently refute the objections so far raised against identification of the Lower Loup Focus with the Pawnee tribes. There is, therefore, no reason whatsoever for abandoning the hypothesis outlined by Strong wherein the Lower Loup Focus is considered a protohistoric phase of Pawnee culture.

LITERATURE CITED

BANDELIER, A. F.

1890. Contributions to the history of the southwestern portion of the United States. Cambridge.

BRUCE, ROBERT.

1932. The fighting Norths and Pawnee scouts.

BUTTERFIELD, C. W.

1881. History of the discovery of the Northwest by Jean Nicolet. Cincinnati.

DORSEY, G. A.

1906. The Pawnee Mythology, pt. 1. Carnegie Inst. of Washington.

DUNBAR, J. B.

1880. The Pawnee Indians: their history and ethnology. *Mag. Amer. Hist.*, vol. 4, no. 4, pp. 241-281.

DUNLEVY, M. L.

1936. A comparison of the cultural manifestations of the Burkett (Nance County) and the Gray-Wolfe (Colfax County) sites. Chapters in *Nebraska Archeology*, vol. 1, no. 2, pp. 149-247. Univ. Nebraska.

GRIFFIN, J. B.

1937. The archeological remains of the Chiwere Sioux. *Amer. Antiquity*, vol. 2, no. 3, pp. 180-181.

GRINNELL, G. B.

1893. Pawnee hero stories and folk-tales. New York.

HAYDEN, F. V.

1868. Notes on Indian history, etc. *Ann. Rep. Smithsonian Inst.* 1867, pp. 411-412.

HILL, A. T., and WEDEL, W. R.

1936. Excavations at the Leary Indian village and burial site, Richardson County, Nebraska. *Nebraska Hist. Mag.*, vol. 17, no. 1.

HOLMES, W. H.

1903. Aboriginal pottery of the eastern United States. 20th *Ann. Rep.*, Bur. Amer. Ethnol., pp. 200-201 and pl. 177.

MURIE, JAMES.

1914. Pawnee Indian Societies. *Anthrop. Pap.*, Amer. Mus. Nat. Hist., vol. 11, pt. 7.

STRONG, W. D.

1935. An introduction to Nebraska archeology. *Smithsonian Misc. Coll.*, vol. 93, no. 10.

THOMAS, A. B.

1935. After Coronado. Univ. Oklahoma Press.

WEDEL, W. R.

1936. An introduction to Pawnee archeology. *Bur. Amer. Ethnol.*, Bull. 112.



1



2

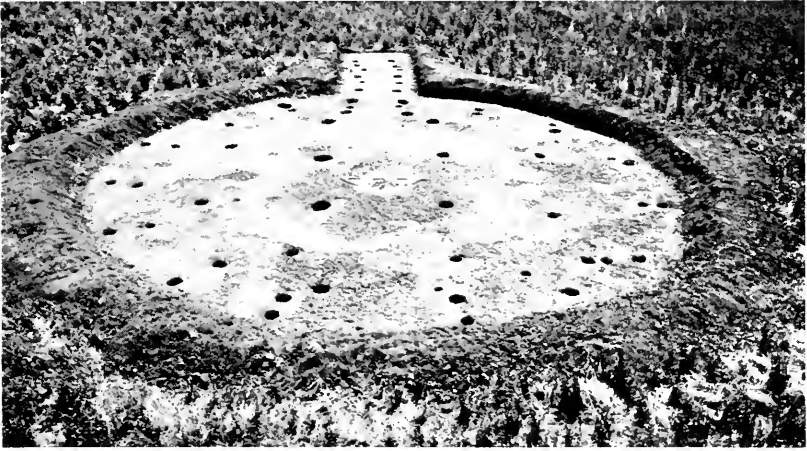
Scenes in the Pawnee village on the Loup River near Genoa, Nebr., in 1871. This was the last northern settlement of the tribe prior to its final removal to the Indian Territory circa 1875. (Photographs by W. H. Jackson.)



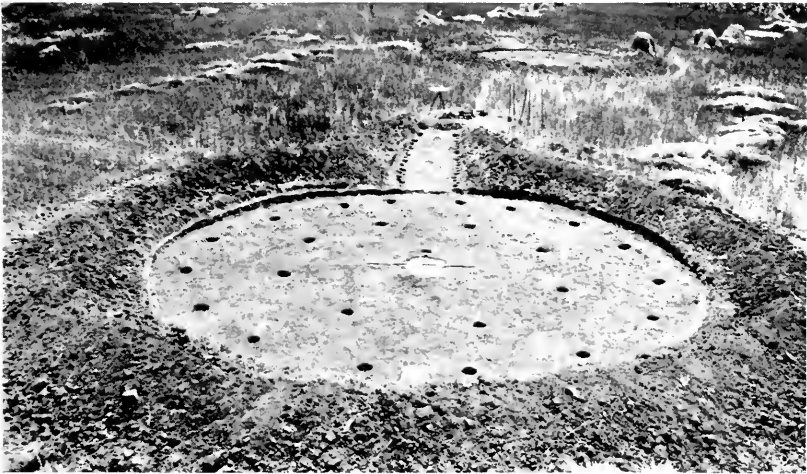
1. The Wright site near Genoa, Nebr., showing type of bluff top village location preferred by the Pawnee in protohistoric times; Beaver Creek valley at right. (Courtesy of the Nebraska State Historical Society.)



2. Excavated floor of protohistoric Pawnee earthlodge showing circular outline, central firepit, postholes, and short vestibule doorway; Wright site. (Courtesy of the Nebraska State Historical Society.)



1. Excavated floor of protohistoric Pawnee earthlodge at Larsen site, on Looking-glass Creek: showing central firepit, surrounded by four primary and three circles of secondary post molds. Note the peculiar arrangement of postholes at the rear of the floor, opposite the entrance, where the family shrine was traditionally placed. (Courtesy of the Nebraska State Historical Society.)



2. Excavated floor of late historical Pawnee earthlodge near Leshara, occupied probably after 1850. This lodge had eight central roof supports, a raised altar platform at the rear directly opposite the doorway, and a sill of baked clay across the inner end of the entrance passage. Another house floor may be seen in the background. (Courtesy of the Nebraska State Historical Society.)



1. Restored pot of late Pawnee type from Archer, Nebr.; height 9 inches. (Courtesy of the Nebraska State Historical Society.)



2. Restored vessel of protohistoric Pawnee type from the Wolfe site near Schuyler; height $4\frac{5}{8}$ inches. (Courtesy of the Nebraska State Historical Society.)



1



2

Restored pottery vessels from the Bellwood site, occupied prior to 1800. Fig. 1 is characteristic of the ware made by the Pawnee during the nineteenth century. Fig. 2 illustrates the cloistered rim frequently found on the better grade of pottery produced in the earlier period. (Courtesy of the Nebraska State Historical Society.)

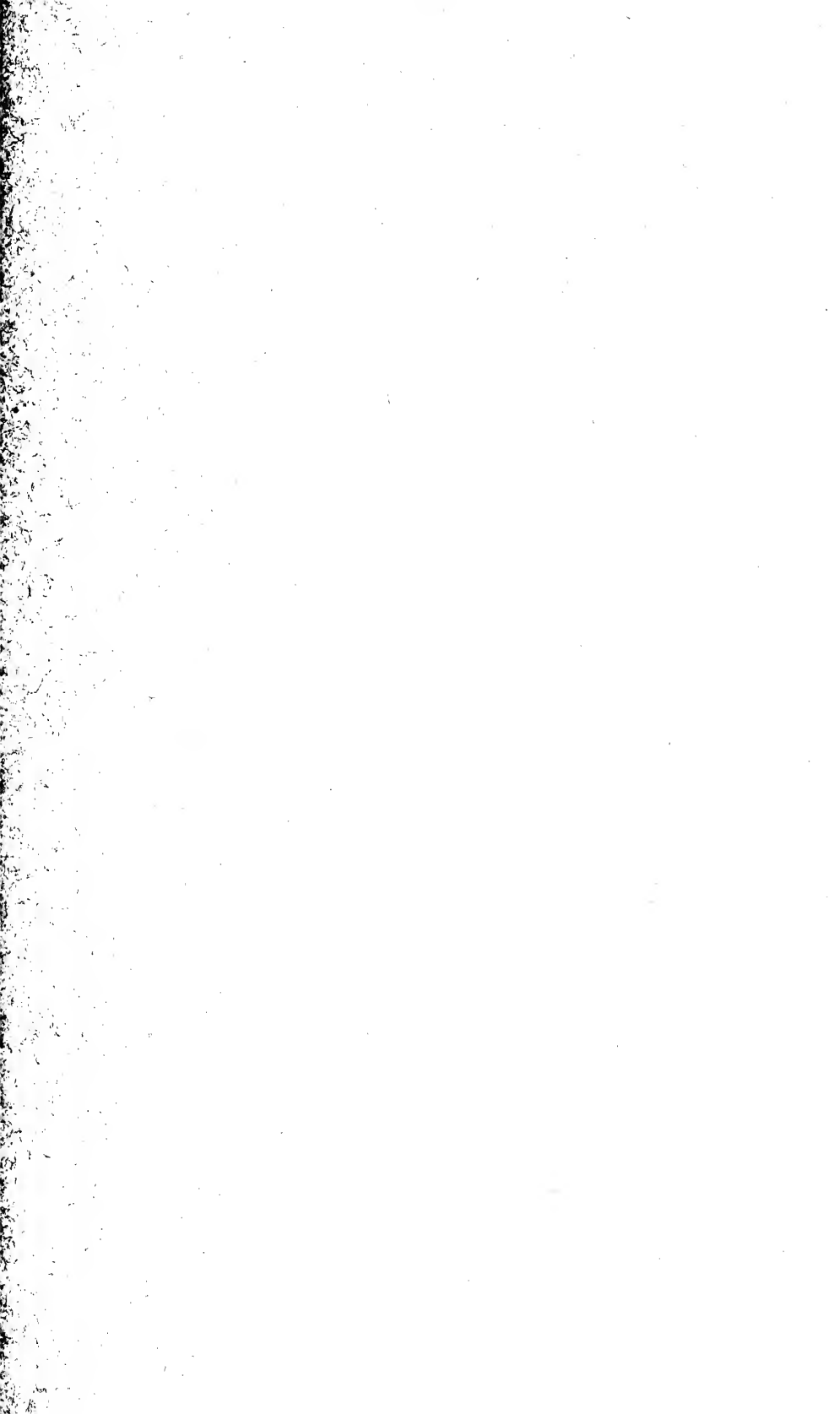


1



2

Restored vessels of late Pawnee type. Fig. 1, 11½ inches high, is from the Bellwood site; Fig. 2 is from Horse Creek site. (Courtesy of the Nebraska State Historical Society.)





SMITHSONIAN MISCELLANEOUS COLLECTIONS
VOLUME 97, NUMBER 8

DRAWINGS BY GEORGE GIBBS IN
THE FAR NORTHWEST,
1849-1851

(WITH 18 PLATES)

BY
DAVID I. BUSHNELL, JR.



(PUBLICATION 3485)

CITY OF WASHINGTON
PUBLISHED BY THE SMITHSONIAN INSTITUTION
DECEMBER 30, 1938



"THE TISH-RÁWA VILLAGE, AND THE KLAMATH, BELOW THE ENTRANCE
OF THE SALMON"

Drawn by Capt. Seth Eastman, from original sketch by George Gibbs,
October 1851.

SMITHSONIAN MISCELLANEOUS COLLECTIONS
VOLUME 97, NUMBER 8

DRAWINGS BY GEORGE GIBBS IN
THE FAR NORTHWEST,
1849-1851

(WITH 18 PLATES)

BY
DAVID I. BUSHNELL, JR.



(PUBLICATION 3485)

CITY OF WASHINGTON
PUBLISHED BY THE SMITHSONIAN INSTITUTION
DECEMBER 30, 1938

The Lord Baltimore Press
BALTIMORE, MD., U. S. A.

ILLUSTRATIONS

PLATES	PAGE
1. "The Tish-ráwa village, and the Klamath, below the entrance of the Salmon." Drawn by Capt. Seth Eastman from original sketch by George Gibbs. October 1851. (Frontispiece)	
2. Shoshonee Falls of Snake River, August 15, 1849. 1. The Cañon below the falls. 2. The falls.....	6
3. Ravine in mountains of Burnt River, Baker County, Oregon. September 4, 1849.....	6
4. On the trail in Oregon. Ascending hill from Deschutes River. October 2, 1849.....	6
5. Burial canoe on bank of the Columbia at mouth of La Camas Creek. October 30, 1850.....	6
6. Canoe on the Columbia River near Oak Point. October 1850.....	6
7. Chiefs of tribes in the valley of the Willamette. 1. Slacum. Chief of tribe at the falls of the Willamette, probably the Clowwewalla. May 1851. 2. Joe or Alquema. Chief of the Santiam band of the Calapooya.	6
8. Valley of the Willamette. 1. Champoege and French Prairie. April 1851. 2. The Willamette at Champoege. May 1851.....	10
9. At Oregon City, 1851. 1. Oregon City and the Falls of the Willamette. 2. Indians taking salmon at the falls of the Willamette. June 1851..	10
10. Hudson's Bay Company's post at Fort Vancouver. July 1851.....	10
11. At the Hudson's Bay Company's Post. 1. Fort Vancouver, July 2, 1851. 2. Catholic Chapel at Fort Vancouver, July 1, 1851. 3. Officers Quarters, Columbia Barracks, July 2, 1851.....	10
12. Sonoma, California. August 11, 1851.....	14
13. Upper end of Clear Lake, California. August 19, 1851.....	14
14. Redwood Tree, 52 feet in circumference. September 6, 1851.....	16
15. Sketches in the valley of the Klamath. 1. Woman and child, at junction of Klamath and Trinity Rivers. October 6, 1851. 2. Young married woman, at junction of Klamath and Trinity Rivers. October 6, 1851. 3. Young girl, Salmon River. November 12, 1851.....	16
16. Views in the valley of the Klamath. 1. The Klamath above the fish dam. October 9, 1851. 2. The Klamath. Signal tree of the Indians. October 13, 1851.....	20
17. The Shaste Butte and Valley. October 27, 1851.....	20
18. Young Chief of the Weit-spek tribe, probably Mec-ug-gra. Drawn by Capt. Seth Eastman from original sketch by George Gibbs. October 1851	26

TEXT FIGURES

1. Carvings in wood and bone from lower Columbia River.....	8
2. Wooden bowl from Shoalwater Bay.....	9
3. Bow, hats, and headband from Klamath River, California.....	16
4. Baskets from Klamath River, California.....	18
5. Spoons and trays from Klamath River, California.....	19

DRAWINGS BY GEORGE GIBBS IN THE FAR NORTHWEST, 1849-1851

BY DAVID I. BUSHNELL, JR.

(WITH 18 PLATES)

INTRODUCTION

George Gibbs, whose drawings form the subject of this article, was born July 17, 1815, at Sunswick, Long Island, New York, near the present Astoria. He died in 1873. At the age of 17, failing to receive the desired appointment to West Point, he accompanied an aunt to Europe, where he devoted 2 years to travel and study. Returning to New York, he soon entered Harvard, where he was graduated in law in 1838, and subsequently entered the law office of Preston Hall. However, the profession did not appeal to him, and during the next few years he wrote several works on historical subjects which were highly acclaimed.

The Far West was now becoming of interest, and the mystery of the wilderness appealed to many. Gibbs was among those who were thus attracted, and in 1849 he accompanied the Mounted Rifle Regiment to Oregon, where he arrived early in October. That same autumn he became deputy collector of customs at Astoria and was later attached to the Indian Commission in Oregon. In 1851 he was a member of the McKee party and visited the northwestern part of California. During the journey he learned much concerning the various native tribes with whom he came in contact, especially those who were encountered in the valley of the Klamath. Later he settled near Fort Steilacoom, Washington, where he devoted much time to the study of the languages of the different tribes and prepared extensive vocabularies which, together with brief lists of words, are now in the Smithsonian Institution. Although interested primarily in linguistic studies, Gibbs collected ethnological material, much of which is preserved in the collections of the National Museum, being among the earliest specimens gathered in the country beyond the Rocky Mountains.

Gibbs was preparing to return to New York and so wrote to his friend, Prof. S. F. Baird of the Smithsonian Institution: "North West Boundary Survey, Fort Walla-Walla, Nov. 16, 1860. I arrived

here yesterday on my way to Washington." He next wrote to Prof. Baird from "261 Greene Street, New York, Feb. 5, 1861," soon after he reached his home.

The correspondence between Gibbs and Professor Baird continued through many years, both while Gibbs was in the west and after his return to New York, and later when he lived in Washington. The letters are most interesting, and many refer, in addition to the work in which both were engaged, to places and persons now known only in history.

WITH THE MOUNTED RIFLE REGIMENT TO OREGON, 1849

As previously mentioned, Gibbs accompanied the Mounted Rifle Regiment to Oregon in 1849, being one of many civilians who reached the valley of the Columbia at that time.¹ The regiment was under command of Brevet-Col. W. W. Loring, and the expedition started "with about 600 men, 31 commissioned officers, several women and children, the usual train agents, guides, and teamsters, 160 wagons, 1,200 mules, 700 horses, and subsistence for the march to the Pacific."

An interesting account of the trip has been preserved;² it was presented as (p. 126): "A report, in the form of a journal, to the Quartermaster General, of the march of the regiment of mounted riflemen to Oregon, from May 10 to October 5, 1849, by Major O. Cross, quartermaster United States army."

Excerpts from the journal will shed light on the dangers and difficulties with which all were confronted:

Major Cross left St. Louis May 10, 1849, and ascended the Missouri to Fort Leavenworth where he arrived 9 days later. "On inquiring at the fort I learned that the troops were ten days in advance of me, which was a very long start, as my mode of travelling was the same as that of the regiment." The next day he left for Fort Kearny. "My outfit was as indifferent a one as ever left for any station, much less the Rocky mountains."

It is not known with which of the groups Gibbs was then traveling, but he was probably with the troops that had left Fort Leavenworth about the time Cross was departing from St. Louis.

¹ Bancroft, Hubert Howe, *The works of . . .* vol. 30, *History of Oregon*, vol. 2, 1848-1888, p. 81. San Francisco, 1888.

² The report was made by Maj. Osborne Cross to Maj. Gen. T. S. Jesup, Quartermaster General, and was incorporated in the report of the latter to C. M. Conrad, Secretary of War. 31st Congr., 2d Sess., Senate Ex. Doc. No. 1, pt. 2, Washington, 1850.

Again the journal (p. 143): "*June 5.*—Large trains could be seen this morning wending their way along on both sides of the Platte. The river here is nearly three miles wide, interspersed with islands, some of which are thinly covered with very small cottonwood and willow." That day the wagons, 160 in number, were overhauled and many were repaired.

June 7.—"To-day buffalo were seen for the first time, which created no little excitement."

June 19.—"I visited Chimney Rock this morning, as the command wended its way along the river."

June 22.—Arrived at Fort Laramie. "Fort Laramie is situated on Laramie's creek, a rapid stream, about 60 yards wide, with a firm, pebbly bottom. This stream rises among the Black Hills to the west, and falls into the North Platte, about half a mile below the fort.

"This fort is built in the form of a quadrangular figure, and of unbaked clay, or adobes; the wall is about twenty feet high, with a small palisading on a part of it. There are two block-houses at the corners, diagonally from each other . . . Over the main entrance, which faces the river, there is also another small block-house. The buildings are made inside, the wall forming a part of them." There were no trees about the fort. Game was formerly plentiful, but "has greatly diminished since emigrants have made it the great thoroughfare to Oregon and California." Fort Laramie is 639 miles from Fort Leavenworth.

August 1.—"It was at the side of the river, and at this place, that I saw the celebrated spring generally known as the Steamboat spring . . . This place is immediately at the point where the two trails turn off for California and Oregon, and within a short distance of the Salt lake . . ."

August 4.—"We descended a long hill, which brought us into a sandy plain, which extends to Fort Hall, and on the banks of the Port Neuf . . ."

August 10.—"Our encampment last evening seemed to be the terminus of Snake River valley, as the appearance of the river entirely changed after a march of about five miles, which brought us to the American falls . . . The scene was truly magnificent . . ." Many rapids in the river, islands and masses of rock in the stream.

August 11.—"We crossed Ogden's river about 12 o'clock. The road turns off to the south for California, which was taken by the Californians who were still along . . ."

August 15.—A day of much interest for Gibbs. Left camp at 4 in the morning and, as the journal continues (p. 196):

We travelled, however, rapidly for about eight miles . . . until we arrived at the creek again. At this place we waited for our wagons, which soon came up; and, having assisted them out of the cañon, which was no easy work, we continued on until the middle of the day, when we again came to the banks of the river, which were at least two or three hundred feet in height. I attempted to descend into the valley through which the river ran, for the purpose of procuring water, but it was so fatiguing, both for myself and horse, that I returned without being able to accomplish it.

It was at this place we could easily hear the sound of a waterfall, which, from the noise, we at first supposed might have been the Little Falls of Snake river; but, as we were still twenty miles from that point, we were soon satisfied that it did not proceed from there, or the small cascade on the opposite bank, which is mentioned by Colonel Fremont as the Subterranean river; and we were much surprised to learn, the next day, that within ten miles of this place there is a cascade, which, in height, is not surpassed by the Niagara Falls. The guide, who was with the command, having travelled this route very often, was shown the place by an Indian, and took Mr. Gibbs, of New York, and Lieutenant Lindsay to the place, who pronounced it one of nature's great wonders. The river here becomes a little contracted, and passes through a chasm of solid rock; it commences to fall about a quarter of a mile above the last pitch, and, after forcing itself among loose rocks which lay in its way, takes a perpendicular pitch of at least 160 feet, and it is even thought to be a greater height. They descended to the foot of the falls, and after much difficulty and some length of time, where they were better able to judge more accurately of its great height; and there seems to be but one opinion, that it equalled in grandeur, in proportion to the column of water, the Niagara Falls. Having been the first who had ever taken the trouble to examine them carefully, and wishing to change the name said to have been given by a priest many years since, they decided on that of the Great Shoshonie falls, instead of Canadian, as being the most appropriate.

The road does not pass there, and probably its nearest point is not less than eight or ten miles, which is probably the reason why it is so little known, for I have never seen it mentioned by those who have trapped in this country for years . . .

We continued our journey until sundown, when we came to the foot of the little falls on Snake river, commonly called the Little Salmon Falls, and encamped for the night immediately on the banks of the river.

The drawings of the falls made by Gibbs that day are reproduced in plate 2. This was the first mention of Gibbs by Major Cross.

The expedition continued through the mountains until (p. 210):

September 4.—Mountains were to be seen all around, and it appeared a mystery how we had extricated ourselves from those left behind us with so little difficulty, or how we were to pass those ahead of us. This brought us again on Burntwood creek, where we encamped for the night . . .

The ravine through which the Burntwood passes is too narrow to be cultivated, but the soil is rich and ought to yield well. The evening was spent in

reaching the tops of some of the highest mountain hills, where the view of the adjacent country well rewarded us for our trouble; a few scattering hemlocks were seen in the ravine where we made our encampment, and the distant hills and ravines beyond were interspersed with several groves of cedar and pine. Our encampment lay in a fork formed by Burntwood creek and a little brook which falls into it . . .³ [Pl. 3.]

The party was now moving in several groups, and it is evident that Gibbs was not always with Major Cross; this explains the difference in the dates that often appear on the sketches made by Gibbs from those of the entries in the journal.

On September 22, Gibbs made a sketch of the Columbia from the mouth of Deschutes River. From this point the wagon train, with which Gibbs must have been traveling, moved southward up the right bank of the Deschutes River. During the morning of October 2, the train ascended the steep cliff near the river. A sketch made at that time reveals the wagons, each drawn by eight mules, forming a long line extending from the camp at the foot of the cliffs to the summit. It is an interesting drawing of a subject seldom recorded (pl. 4).

Leaving the Deschutes River, the expedition passed through the Cascade Range, and, on October 5, Gibbs made several sketches of the forest scenery, to which he attached the legends: "Burnt forest in Cascade Mts.," and "Cascade Mts. Cedar & firs," and again on October 9, "Forests of the Cascade Mts. Cedar & fir."

The expedition had now arrived at its destination. Gibbs continued on to Astoria where he became Deputy-collector of Customs, soon to become attached to the Indian Commission.

ON THE COLUMBIA RIVER, AUTUMN OF 1850

Two drawings of exceptional interest, made by Gibbs on the banks of the Columbia during the month of October 1850, are reproduced in plates 5 and 6.

The first of these shows the "Prow of dead Canoe on Bank of Columbia river, at mouth of Chamus Creek," and is a beautiful example of Gibbs' work. Chamus Creek is believed to have been the stream now known as La Camas Creek, which flows into the Columbia River near the southeast corner of Clarke County, Washington, about 15 miles above Vancouver. This was within the Chinookan country. Whether this canoe was placed on a scaffold or rested on

³ Burnt River flows eastward and joins Snake River in the southern part of Baker County, Oregon.

the ground is not known, but as so little has been recorded concerning the burial customs of the people of the region this sketch is of special interest.

A brief reference to the strange form of burial was made by Lieutenant Broughton, of the Vancouver Expedition,⁴ who explored the lower Columbia during the autumn of 1792. He was near Cape Disappointment, on the Washington side of the mouth of the Columbia, and wrote (vol. 2, p. 54): "At this place was found the remains of a deserted Indian village, and near it three large canoes supported from the ground, each containing dead human bodies. These canoe coffins were decorated at the head and stern with rude carved work, and from their decayed state seemed to have been thus appropriated for a great length of time."

Soon the Lewis and Clark party reached the valley of the Columbia. They encountered the same peculiar burials and left a more detailed account of the manner in which the canoes were placed, and of the various objects deposited in them.⁵ They stated (p. 429):

The Chinooks, Clatsops, and most of the adjoining nations, dispose of the dead in canoes. For this purpose a scaffold is erected, by fixing perpendicularly in the ground four long pieces of split timber. These are placed two by two, just wide enough apart to admit the canoe, and sufficiently long to support its two extremities. The boards are connected by a bar of wood run through them at the height of six feet, on which is placed a small canoe, containing the body of the deceased, carefully wrapped in a robe of dressed skins, with a paddle, and some articles belonging to the deceased, by his side. Over this canoe is placed one of a larger size, reversed, with its gunwale resting on the crossbars, so as to cover the body completely. One or more large mats of rushes or flags are then rolled round the canoes, and the whole secured by cords usually made of the bark of the white cedar. On these crossbars are hung different articles of clothing, or culinary utensils. The method practised by the Killamucks differs somewhat from this; the body being deposited in an oblong box, of plank, which, with the paddle, and other articles, is placed in a canoe, resting on the ground.

Later accounts of the curious form of burial are to be found, but the earlier descriptions are usually the more interesting. However, as remarked in the Lewis and Clark journal (p. 429), "Those who first visit the ground, can only be expected to furnish sketches rude and imperfect."

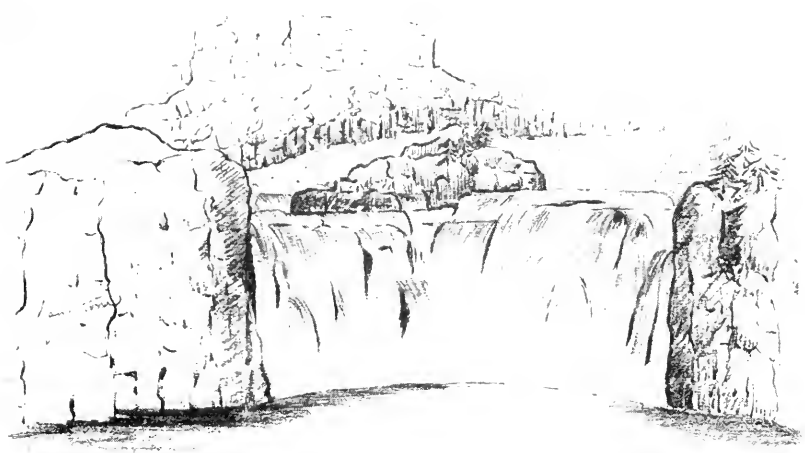
⁴ Vancouver, Captain George, *Voyage of Discovery* . . . 3 vols. London, 1798.

⁵ Lewis and Clark, *Travels to the source of the Missouri river and across the American continent to the Pacific ocean* . . . in the years 1804, 1805, and 1806. London, 1814.

Shoshone Falls of Snake River August 15, 1849



1. The cañon below the Falls.



Shoshone Falls of Snake River August 15, 1849

2. The Falls.

SHOSHONEE FALLS OF SNAKE RIVER, AUGUST 15, 1849



Ravine in the Mts of Burnt
River of the Camp of Sept 4.
1849.

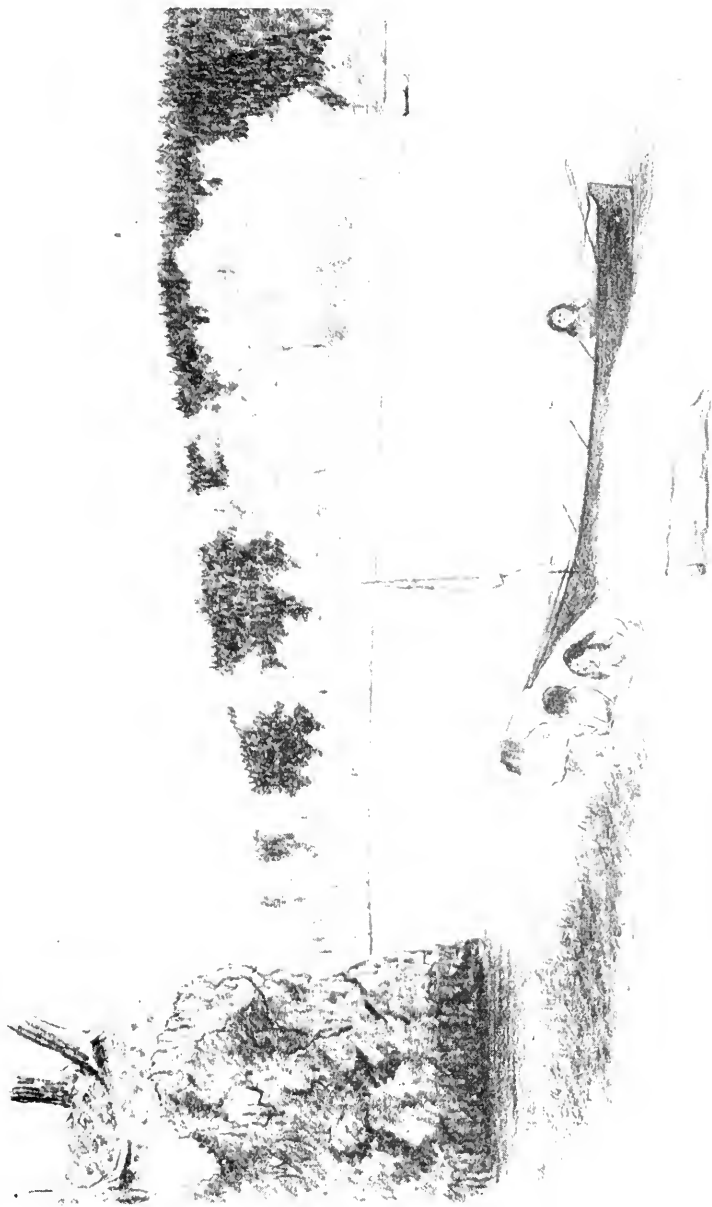
RAVINE IN MOUNTAINS OF BURNT RIVER, BAKER COUNTY, OREGON,
SEPTEMBER 4, 1849



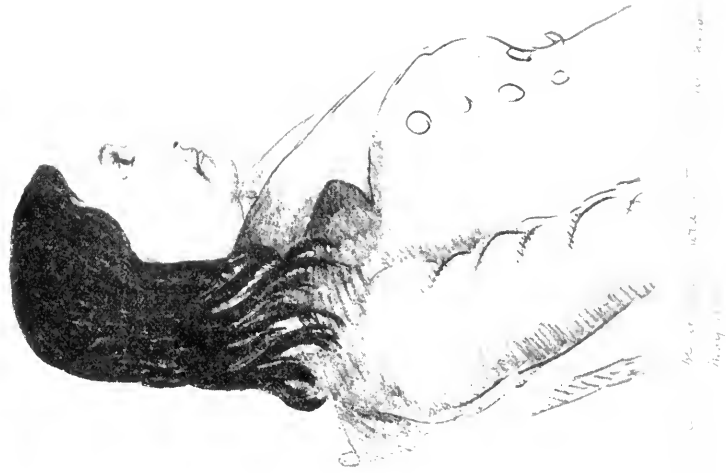
ON THE TRAIL IN OREGON: ASCENDING HILL FROM DESCHUTES RIVER. OCTOBER 2, 1849



BURIAL CANOE ON BANK OF THE COLUMBIA RIVER AT MOUTH OF
LA CAMAS CREEK. OCTOBER 30, 1850



CANOE ON THE COLUMBIA RIVER NEAR OAK POINT. OCTOBER 1850



1. Slacum, Chief of tribe at the falls of the Willamette, probably the Clowwewalla. May 1851.



2. Joe or Alouena, Chief of the Santiam band of the Calapooya.

As previously mentioned, it is not known whether the canoe, the prow of which was sketched by Gibbs, was placed on a scaffold when in use or had always rested on the ground as shown in the drawing. The drawing suggests that the prow was rather massive and heavy, but there is no way to judge its size.

The Chinookan tribes who occupied both banks of the lower Columbia excelled in carving wood and bone. On January 20, 1806, when near the mouth of the Columbia on the south side, the Lewis and Clark party were among the Clatsops with whom they maintained a friendly intercourse. The narrative of the expedition refers to the skill of the natives in making many articles used in and about their houses, described as "large wooden buildings, varying in length from twenty to sixty feet, and from fourteen to twenty in width." The narrative continues (p. 432):

They are . . . very dexterous in making a variety of domestic utensils, among which are bowls, spoons, skewers, spits, and baskets. The bowl or trough is of different shapes, sometimes round, semicircular, in the form of a canoe, or cubic, and generally dug out of a single piece of wood, the larger vessels having holes in the sides by way of handles, and all executed with great neatness. In these vessels they boil their food, by throwing hot stones into the water, and extract oil from different animals in the same way. Spoons are not very abundant, nor is there any thing remarkable in their shape, except that they are large and the bowl broad . . . The usual plate is a small mat of rushes or flags, on which every thing is served.

Later, when the expedition was at the Cathlamah village, also on the Columbia and not far from the Clatsops, certain customs of the people were recorded in the narrative (p. 493):

This village we have already described, as situated opposite to the seal islands: on one of these the Indians have placed their dead in canoes, raised on scaffolds, above the reach of the tide. These people seem more fond of carving in wood than their neighbours, and have various specimens of their taste about the houses. The broad pieces supporting the roof and the board through which doors are cut, are the objects on which they chiefly display their ingenuity, and are ornamented with curious figures, sometimes representing persons in a sitting posture supporting a burden.

Beautiful examples of the work of the people near the mouth of the Columbia are shown in figure 1. Three of the carvings are in wood and one in bone. The latter, a knife handle, has on the end a remarkable representation of a raccoon, *Procyon lotor*, with the eyes indicated by copper inlays. The club is made of cedar and is rather light for the purpose indicated. All were collected by George Gibbs probably in 1850 or 1851. Another bowl obtained by him in the vicinity of Shoalwater Bay, on the coast a short distance north of

the mouth of the Columbia, is reproduced in figure 2. Similar pieces were undoubtedly seen by Lewis and Clark a generation earlier.

The second sketch made during the autumn of 1850, plate 6, bears the legend "Columbia River near Oak Point, Oct. 1850." The point is on the right bank of the Columbia about midway between the mouth and Vancouver, and was so named by Lieutenant Broughton in 1792.⁶ When going up the river they arrived at a spot "where, for the first

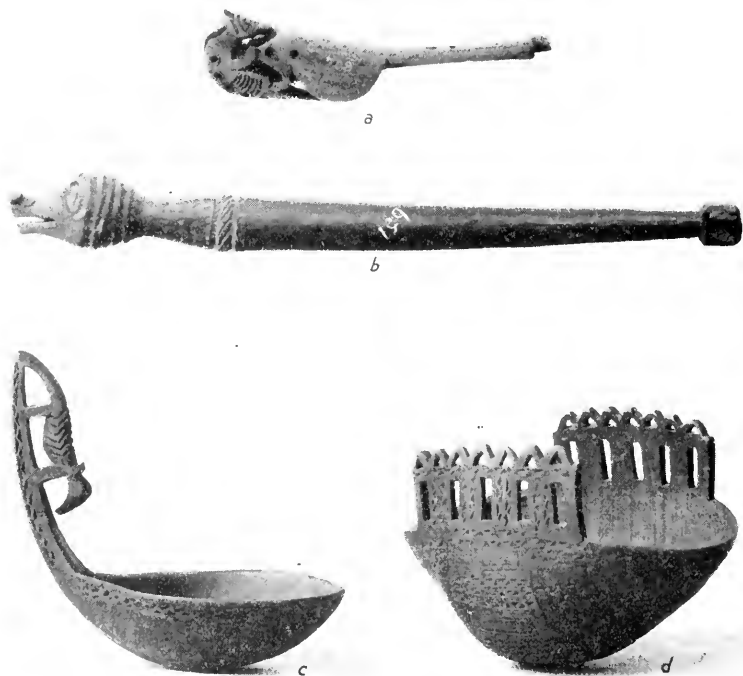


FIG. 1.—Specimens collected by George Gibbs on the lower Columbia.

a, bone knife handle, length $8\frac{1}{2}$ inches, U.S.N.M. no. 708; *b*, club for killing fish, wood, length 18 inches, U.S.N.M. no. 651; *c*, spoon, wood, length of figure on handle $3\frac{7}{8}$ inches, no number; *d*, bowl, wood, diameters 6 and 8 inches, U.S.N.M. no. 691.

time in this river, some oak-trees were seen, one of which measured thirteen feet in girth; this obtained the name of Oak Point."

The canoe is the most interesting feature of the sketch. To quote again from Lewis and Clark ⁷ (pp. 433-434):

The industry of the Indians is not confined to household utensils: the great proof of their skill is the construction of their canoes. In a country, indeed, where so

⁶ Vancouver, op. cit. vol. 2, p. 61.

⁷ Op. cit.

much of the intercourse between different tribes is carried on by water, the ingenuity of the people would naturally direct itself to the improvement of canoes, which would gradually become, from a mere safe conveyance, an elegant ornament. We have accordingly seen, on the Columbia, canoes of many forms, beginning with the simple boats near the mountains, to those more highly decorated, because more useful nearer the mouth of the Columbia. Below the grand cataract there are four forms of canoes: the first and smallest is about fifteen feet long, and calculated for one or two persons: it is, indeed, by no means remarkable in its structure, and is chiefly employed by the Cathlamahs and Wahkiacums among the marshy islands. The second is from twenty to thirty-five feet long, about two and a half or three feet in the beam, and two feet in the hold. It is chiefly remarkable in having the bowsprit, which rises to some height above the bow, formed by tapering gradually from the sides into a sharp point. Canoes of this shape are common to all the nations below the grand rapids.

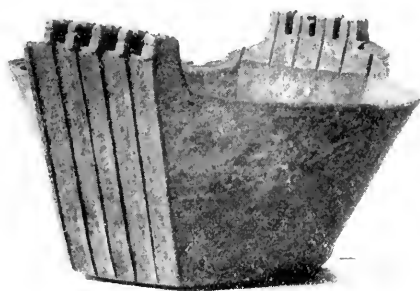


FIG. 2.—Wooden bowl collected by George Gibbs at Shoalwater Bay. Diameters $8\frac{1}{2}$ and $10\frac{1}{2}$ inches, U.S.N.M. no. 692.

The other types of canoes, larger than those just described, need not be mentioned. Evidently the canoe sketched by Gibbs belonged to the second group mentioned by Lewis and Clark, those which were “common to all the nations below the grand rapids.” There is no allusion in the early narratives to the use of sails and masts in the native craft. The mast and sail shown in the sketch had been adopted after contact with Europeans.

OREGON, 1851

A letter from the Acting Commissioner of Indian Affairs, dated October 25, 1850, addressed to J. P. Gaines, A. H. Skinner, and Beverly S. Allen, stated³ (p. 114):

³ *In Annual Report of the Commissioner of Indian Affairs . . . 1850. Washington, 1850.*

"Gentlemen: I have been officially notified of your appointment as 'Commissioners to negotiate treaties with the several Indian tribes in the Territory of Oregon, for the extinguishment of their claims to lands lying west of the Cascade Mountains, under the act of 5th June last'; and am directed by the Hon. Secretary of the Interior to prepare appropriate instructions for your observance in the discharge of the duties of your office." The region was briefly described, the tribes were mentioned in a vague manner, and the letter then continued: "It will probably be best for you to treat first with the Indians in the white settlements, particularly in the Willamette Valley—and to treat separately with each tribe . . ."

Evidently the three commissioners were active during the ensuing months. In a joint communication to the Commissioner of Indian Affairs, dated Champoly, April 19, 1851,⁹ they transmitted (p. 205): "a treaty concluded, on the 16th instant, with the Santiam band of the Callapooya tribe of Indians, by which they cede to the United States a portion of the Willamette valley, about eighty miles in length and about twenty in width. And also a treaty, concluded this day, with the Twallalty band of the same tribe, including a country about fifty miles in length and about thirty in width . . . Their numbers are, of the Santiam band, 155, and of the Twallaltys, 65."

Gibbs was associated with the Commissioners when the treaties were made.

Among the Gibbs material in the Bureau of American Ethnology, Smithsonian Institution, is a manuscript designating where and when he prepared many of the vocabularies. One record is of interest at this time as it refers to events at Champoeg in April 1851:¹⁰

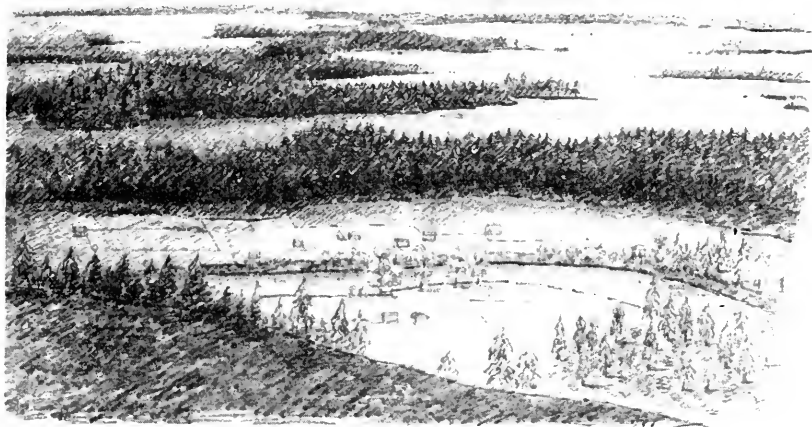
Kalapuya.—My own vocabulary of this language was obtained April 4, 1851, while the Commission was engaged in a treaty with them at Champoeg. It is of the Si-yam-il, or as generally called Yamhill band, living on the river of that name, which empties into the Willamet from the coast range. The Twallatys (Twalati), and the Luckamukes (Luk-a-mai-yuk) speak the same dialect. The Santiam band, on the east side of the Wilamet, a rather different one. It was given by Thomas and Antoine, Chiefs.

Molele.—Obtained at the same place. This was received from an Indian of the band inhabiting the upper waters of the Santiam.

Many drawings were made at this time, four of which are now reproduced. Others show different parts of the valley as it appeared during the spring of 1851.

⁹ In Annual Report of the Commissioner of Indian Affairs . . . 1851. Washington, 1851.

¹⁰ Bur. Amer. Ethnol. Manuscript Catalog No. 742.

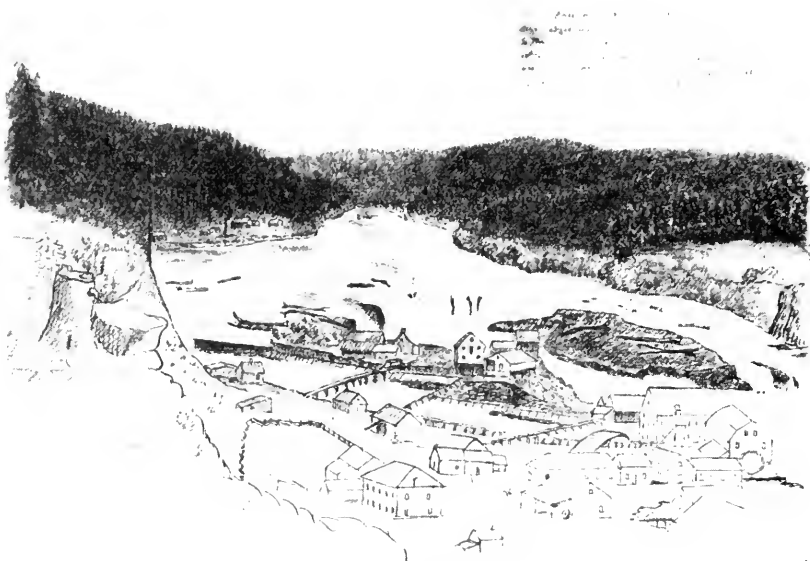


1. Champoeg and French Prairie, April 1851.



2. The Willamette River at Champoeg, May 1851.

VALLEY OF THE WILLAMETTE



1. Oregon City and the Falls of the Willamette.

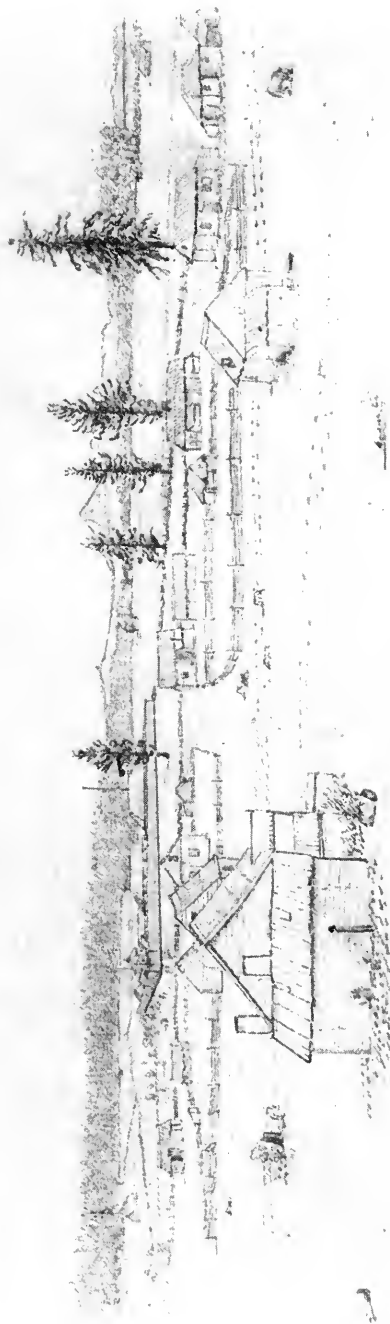


2. Indians taking salmon at the Falls of the Willamette, June 1851.

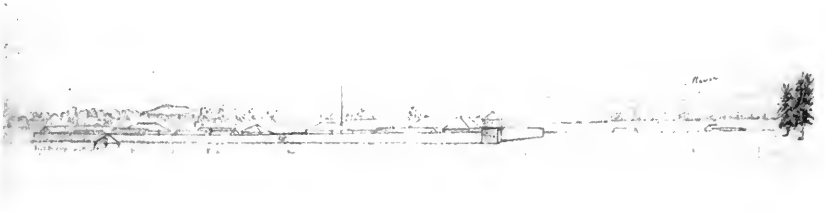
AT OREGON CITY, 1851

*General view of Hudson's Bay Company's Post
at Fort Vancouver, Oregon, with the "Kanaka
Village" July 1851.*

920.1.

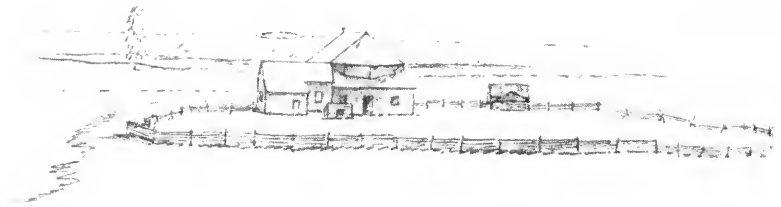


HUDSON'S BAY COMPANY'S POST AT FORT VANCOUVER, JULY 1851



*Hudson's Bay Co. Fort, 1851.
July 2^d 1851.*

1. Fort Vancouver, July 2, 1851.



*Catholic Chapel, Fort Vancouver,
July 2^d 1851.*

2. Catholic Chapel at Fort Vancouver, July 1, 1851.



*Officers' quarters, Columbia Barracks,
July 2^d 1851.*

3. Officers' quarters, Columbia Barracks, July 2, 1851.

AT THE HUDSON'S BAY COMPANY'S POST

Portrait sketches of two chiefs are given in plate 7, one being that of a chief of the Santiam band of the Callapooyas, but not one who had contributed to the vocabulary. This is well drawn, and the sloping forehead reveals the effect of artificial flattening. It was probably a good likeness.

The second portrait is that of "Slacum, Chief of tribe at Falls of Willamette (Upper Chinooks)," and was drawn a few days after the treaty was made with the Callapooya. Slacum may have been a chief of the Clowwewalla, belonging to the Chinookan family, a tribe that occupied the region bordering the falls of the Willamette River, the site of Oregon City. The name Slacum was probably derived from that of an American naval officer who visited the region in 1836 "to obtain information in relation to the settlements on the Oregon river."¹¹ He prepared an interesting, although brief, account of the native tribes then living on the Willamette, part of which follows. When ascending the river:

The first tribe of Indians are the Kallamooks, on the left bank, on a small stream of the same name, 30 miles from its mouth: 2d are Keowewallahs, alias *Tummevcatas* or Willhametts. This tribe, now nearly extinct, was formerly very numerous, and live at the falls of the river, 32 miles from its mouth, on the right bank. They claim the right of fishing at the falls, and exact a tribute from other tribes who come hither in the salmon season (from May till October). Principal chiefs deceased. This river at the present day takes its name from this tribe. 3d. "Kallapooyahs" occupy lodges on both sides of the river. 4th. "Fallatrahs" on a small stream of same name, right or west bank. 5th. Champoicho—west bank. 6th. Yamstills—west bank. 7th. Leelahs—both sides. 8th. Hanchoicks. All these 5 tribes speak Kallapooyah dialects, and are doubtless of that tribe, but at present are divided as designated, and governed by chiefs as named. All these tribes do not exceed 1,200.

The Willamette was a beautiful stream, as Slacum wrote, "even in midwinter, you find both sides clothed in evergreen, presenting a more beautiful prospect than the Ohio in June . . . On the right the land rises gradually from the water's edge, covered with firs, cedar, laurel, and pine. The oak and ash is at this season covered with long moss, of a pale sage green, contrasting finely with the deeper tints of the evergreens."

Gibbs appreciated the beauty of the region and revealed it in two sketches reproduced in plate 8.

The first is a view of "Champoeg and the prairies beyond," looking over the Willamette; the second shows the banks of the stream with the variety of trees and shrubs, with spring foliage.

¹¹ Slacum, William A., Memorial of . . . praying compensation for his services . . . 25th Congress, 2d Session, Senate Doc. 24. Washington, 1838.

Champoege was on the right bank of the Willamette, at the northern end of French Prairie, the origin of which name was explained by Bancroft,¹² who wrote (pp. 70-73):

As their terms of contract expired, the Hudson's Bay Company began to retire its servants, giving them choice lands not too far removed from its benign rule. This was the origin of the French Canadian settlements in the beautiful Valley Willamette . . . French Prairie, the tract where the servants of the fur company began their planting in the Willamette Valley, extended from the great westward bend of that river south to Lac La Biche about twenty-five miles . . . The landing at the crossing of the Willamette on the east side was known as Campement du Sable, being a sandy bluff and an encampment at the point of arrival or departure for French Prairie. Two miles above this point was Champoege, the first settlement.

The falls of the Willamette, when surrounded by the primeval forest and in its natural condition, was a place of great beauty. And as it was here that many Indians from the scattered villages would come to get their supply of salmon, it was likewise a place of great importance to the native inhabitants of the valley. But about the year 1840 a settlement was begun at the falls, Oregon City, and soon all was changed, although the few remaining Indians continued to take salmon at the falls, as others had done through generations.

Two sketches by Gibbs, reproduced in plate 9, show the falls, and Oregon City as it appeared in June 1851. An Indian is portrayed spearing fish from a canoe, another is seen standing on a fishing stage, in the right center of the sketch, using a net at the foot of the falls. Fish are also shown leaping from the water. The upper drawing is a view of Oregon City with the falls just beyond.

Oregon City was visited by Major Cross on October 5, 1849, after the completion of the trip from Fort Leavenworth¹³ and was described in these words (pp. 227-228):

The city of Oregon is not a very prepossessing place in its appearance, for, like all new places in the western country, the stumps and half-burnt trees lie about in every direction. It is immediately at the Willamette Falls, hemmed in by the river in front, and a ledge of rocks immediately in rear and very close to the city.

Leaving Oregon City, Gibbs evidently continued down the Willamette and next visited Fort Vancouver, which had been erected during the years 1824-1825. Sketches of the fort, and one of Columbia Barracks a short distance away, are shown in plates 10, 11.

¹² Bancroft, Hubert Howe, *The works of . . .* vol. 29, *History of Oregon*, vol. 1. San Francisco, 1886.

¹³ *Op. cit.* In 31st Congr., 2d Sess., Senate Ex. Doc. No. 1, pt. 2, Washington, 1850.

A concise description of Fort Vancouver, printed in 1840,¹⁴ explains many of the details of the drawings. To quote (pp. 19-20) :

On the north side of the Columbia, and a quarter of a mile from it, stands *Fort Vancouver*, the principal establishment of the Hudson's Bay Company west of the Rocky Mountains. It consists of a number of wooden buildings within a stockade, serving as dwelling-houses, stores, magazines, and workshops; and near it are other small buildings inhabited by the laborers, together with a saw-mill and grist-mill. The whole number of residents at the place is about eight hundred, of whom a large proportion are Indians or half-breeds. Several hundred acres of land near the fort are under cultivation, producing wheat, barley, oats, pease, potatoes, &c., in abundance; and the stock of cattle is also considerable.

It was a place of great activity, surrounded by many tribes who spoke different languages and had strange manners and ways of life.

Maj. Osborne Cross mentioned Fort Vancouver in his journal:¹⁵

Fort Vancouver, which is the headquarters of the Hudson's Bay Company, is on the right bank of the river. It is situated on a beautiful plain, about five miles long, and probably is three quarters of a mile wide. The country gradually rises, and runs back for ten or fifteen miles, passing through several plains, some of which are cultivated. On one of these plains there is an excellent seminary, where the children from the fort and the neighborhood are educated.

Immediately in rear of the fort, and on the rising ground, the company of artillery under Brevet Major Hatheway have put up temporary quarters, and have made themselves very comfortable.

The latter became Columbia Barracks, and the temporary quarters were soon replaced by others of a more permanent nature. The Officers' Quarters at the barracks, as they appeared 2 years later, were sketched by Gibbs July 2, 1851 (pl. 11, fig. 3). At that time they formed an attractive group of buildings facing Fort Vancouver, with the Columbia beyond, while a short distance in the rear was the edge of the forest which extended off to the north.

Gibbs did not remain many days in the vicinity of the fort, but turned southward to California where he joined the McKee party and soon set out to explore the northwestern part of the State and to visit the many native tribes some of whom may never before have come in contact with the white man.

IN NORTHWESTERN CALIFORNIA, 1851

The journal of the expedition into northwestern California, prepared by Gibbs and later mentioned by McKee in his letter of March

¹⁴ Greenhow, Robert, *Memoir, historical and political, on the Northwest coast of North America* . . . 26th Congr., 1st Sess., Senate Doc. 174. Washington, 1840.

¹⁵ *Op. cit.*, p. 228.

13, 1852, was published by Schoolcraft the following year.¹⁶ It is a valuable account of a journey through a part of the country never before carefully studied, and describes briefly the native inhabitants of the rough, mountainous region who occupied secluded valleys in the vicinity of the rivers, often difficult to discover.

Pencil sketches made by Gibbs of scenes along the route reveal much of interest and beauty encountered in the wilderness and are now reproduced for the first time. Statements in the journal which tend to describe or explain the drawings will be quoted, although much of equal value, but not referring to the sketches, must necessarily be omitted.

This will be followed by excerpts from McKee's account of the expedition.

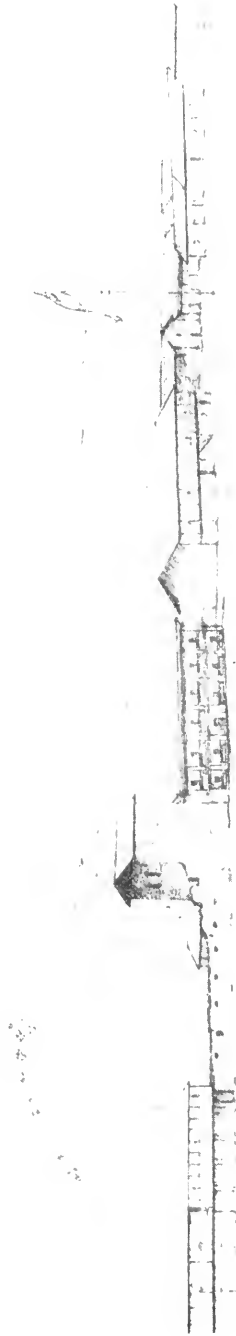
JOURNAL OF THE EXPEDITION OF COLONEL REDICK M'KEE, UNITED STATES INDIAN AGENT, THROUGH NORTH-WESTERN CALIFORNIA. PERFORMED DURING THE SUMMER AND FALL OF 1851. BY GEORGE GIBBS.

Monday, Aug. 11.—Colonel M'Kee and party, escorted by Major Wessells, and a detachment of thirty-five mounted riflemen, left Sonoma this morning, and moved over to Santa Rosa, encamping a little beyond Carillo's ranch . . . The general route proposed to be followed by the expedition, was up Russian river to its sources, down Eel river to Humboldt bay, and thence over to the Klamath, ascending that to the neighborhood of Shasté Valley, should the season permit. [Pl. 12.]

Continuing northward, the party soon reached Clear Lake where they remained several days. Large groups of Indians assembled, and a treaty was entered into. "In personal appearance, many of the Clear Lake Indians are of a very degraded caste; their foreheads naturally being often as low as the compressed skulls of the Chinooks . . . A vocabulary of this language was obtained from the Indian who accompanied us, and who spoke Spanish sufficiently to be enabled to interpret with his people." On the next day, August 19, the proposed treaty was explained to the assembled Indians. A region of great natural beauty (p. 109):

Surrounded on every side by mountains, this valley is completely isolated from the adjoining country, there being no access except by difficult trails . . . The principal valley upon the lake is that upon which we encamped, lying on the western side, and extending from mount M'Kee towards the head. The extent of this may be stated at ten miles in length, by an average width of four. A more beautiful one can hardly be pictured. Covered with abundant

¹⁶ Schoolcraft, Henry R., Information respecting the history, condition and prospects of the Indian tribes of the United States, pt. 3, pp. 99-177. Philadelphia, 1853.



Don Salmar. La Iglesia

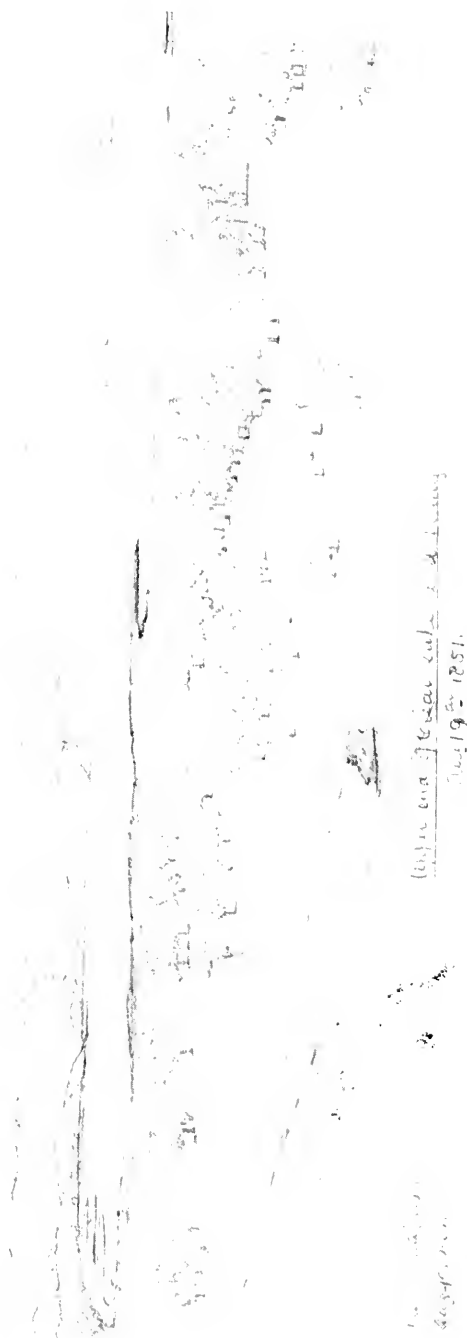
Don Salmar. La Iglesia

Plaza at Sonoma, Cal.

1851

G. C. W.

SONOMA, CALIFORNIA, AUGUST 11, 1851



Upper end of Clear Lake
Aug 19th 1851.

grass, and interspersed with groves of superb oaks of the most varied and graceful forms, with the lake and its green margin of tulé in front, and the distance bounded everywhere by precipitous ranges, it combines features of surpassing grandeur and loveliness. Flowers of great variety and elegance abound, the woods are filled with game, and in the season innumerable flocks of water-fowl enliven the shores. [Pl. 13.]

Wednesday, Aug. 20.—The council was again assembled, and the treaty explained to them as engrossed . . . As regards the suitableness of the reservation for its purpose, there can hardly be a doubt. The spot is isolated to a degree unusual even on the Pacific; abounds in all that is necessary for a large number of people in their savage state, and is capable of being made in the highest degree productive by cultivation.

Saturday, Aug. 30.—This valley, called by the Indians Ba-tem-da-kai, we supposed to be on the head of the south fork of Eel river, and so were informed by our guide and other mountaineers; but a belief exists, as we afterwards found . . . that it is, on the contrary, the head of the river before spoken of as entering the coast to the westward . . . A few Indians visited us, and were directed to call in the adjacent tribes.

The entire party remained in camp the following day.

Sunday, Aug. 31.—Quite a number of Indians were assembled and presents distributed, but no treaty attempted; for our Clear Lake interpreter, although able to comprehend them, could not explain freely in turn. Their language, however, is clearly of the same family as that of the tribes at the head of Russian river, and those last encountered. The total number in the vicinity, as near as could be ascertained, was about six hundred souls . . . They pluck their beards, and some of them tattoo. Many had their hair cut short, but others wore it turned up in a bunch in front, or occasionally on the back of the head . . . The average height of these men was not over five feet four or five inches . . . We saw no women . . .

I took the opportunity of to-day's halt, to ascend the hills on the eastern side of the valley. The view from this point was beautiful, the stream winding in serpentine form along the margin of the plain, fringed with oaks and firs, and the long slopes beyond diversified with forest and prairie. To the east rose heavy ranges of mountains, between which and the yet more distant Sacramento chain, a wide and deep gap indicated another valley, supposed to be the source of the main fork of Eel river.

The next day the trail led through a mountainous section, "crossing deep arroyas and then ascending a broken ridge between the waters of the south and middle forks [of Eel river]." Some Indians were encountered who "had robes of deer skin, dressed with the hair on, over their shoulders. They belonged to a wild mountain tribe, the terror of the valley Indians . . . Of their language and affinities, nothing is known."

September 5.—The trail crossed the river and passed a grove of redwoods. During the day a few Indians were encountered, and (p. 123):

two or three of them were of larger stature than usual, and one was really a fine-looking young fellow. They wore the deer-skin robe over the right

shoulder, and carried the common short bow, backed with sinew [a, fig. 3], and arrows pointed with stone, both tolerably well made. With all these Indians, the arrow-points are fastened into a short piece of wood, which in turn is fixed, though but loosely, into the shaft. The quiver, of dressed deer-skin, holds both bow and arrows. They had also, suspended round the neck, small nets, neatly made after the fashion of the common game-bag; the twine, which was very even, being of course their own work.

The last part of our march led us into a thick redwood forest.

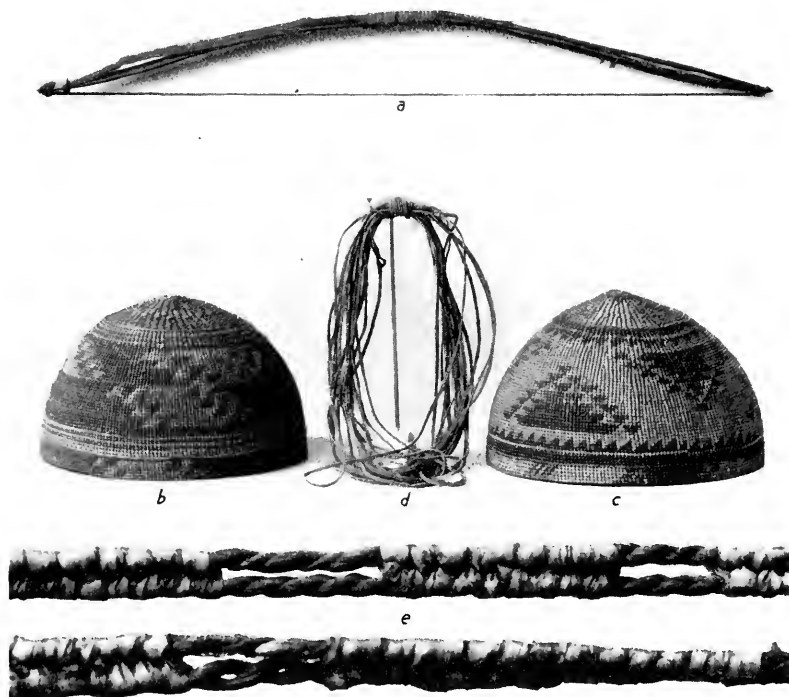


FIG. 3.—Specimens collected by George Gibbs on the Klamath River, California.

a, sinew-backed bow, length 34 inches, U.S.N.M. no. 649; b, basketry hat, diameter 7 inches, depth 4 inches, U.S.N.M. no. 7556; c, basketry hat, diameter $7\frac{3}{4}$ inches, depth 4 inches, U.S.N.M. no. 7558; d, headband, U.S.N.M. no. 7520; e, two sections of d, \times approximately 2.5.

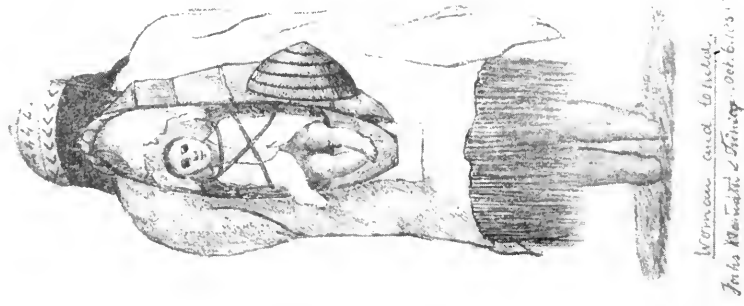
Saturday, September 6.—Indians visited the camp but they were of little interest, and (p. 124):

I endeavored in vain to get from them the names of articles at hand, parts of the body, &c., as they either could not or would not understand the object of the inquiry; nor was our Clear Lake Indian more successful after his method . . .

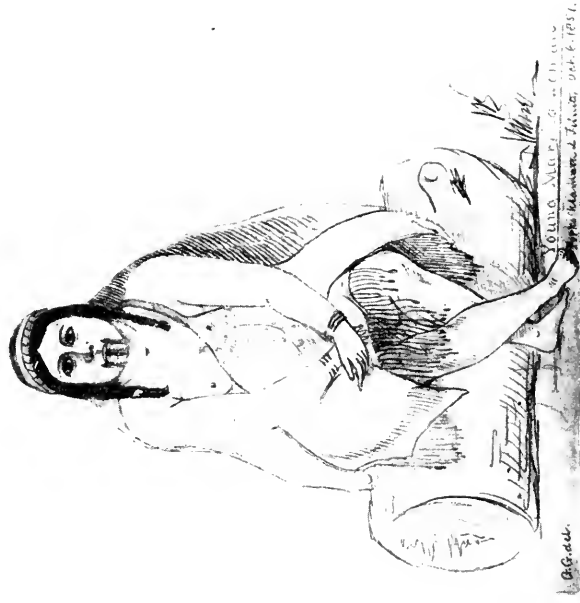


Redwood 1106 Sept 6 1851

REDWOOD TREE, 52 FEET IN CIRCUMFERENCE. SEPTEMBER 6. 1851



1. Woman and child, at junction of Klamath and Trinity Rivers, October 6, 1851.



2. Young married woman, at junction of Klamath and Trinity Rivers, October 6, 1851.



3. Young girl, Salmon River, November 12, 1851.

Our camp was a very pretty one, the little prairie being level and rich, and encircled by a magnificent redwood forest. One tree near the tents I measured, and found it to be fifty-two feet in circumference, at four or five feet from the ground, and this although the bark and a portion of the wood were burned away . . . [Pl. 14.]

From September 29 until the morning of October 9, the party occupied a camp established at the junction of the Klamath and Trinity Rivers. Gibbs did not make a separate entry for each day spent at the camp, but between the days mentioned devoted much time to the study of the Indians with whom he was in contact. Many tribes were represented at the gathering, possessing similar manners and ways of life. To quote briefly (p. 139) :

With regard to their form of government, at least that of the Klamath and Trinity tribes, the *mow-ce-ma*, or head of each family, is master of his own house, and there is a *sci-as-lau*, or chief, in every village . . . The lodges of these Indians are generally very well built; being made of boards riven from redwood or fir, and of considerable size, often reaching twenty feet square. The roofs are pitched over a ridge-pole, and sloping each way; the ground being usually excavated to the depth of three or four feet, and a pavement of smooth stones laid in front. The cellars of the better class are also floored and walled with stone. The door always consists of a round hole in a heavy plank, just sufficient to admit the body; and is formed with a view to exclude the bears, who in winter make occasional and very unwelcome visits.

The people were described as being superior to any previously met, and with countenances denoting greater force and energy of character, as well as intelligence . . . The superiority, however, was especially manifested in the women, many of whom were exceedingly pretty; having large almond-shaped eyes, sometimes of a hazel color . . . their only dress the fringed petticoat, or at most, a deer-skin robe thrown back over the shoulders, in addition. The petticoat with the wealthier, or perhaps more industrious, was an affair on which great taste and labor were expended. It was of dressed deer-skin; the upper edge turned over and embroidered with colored grasses, the lower cut into a deep fringe, reaching nearly to the knee, and ornamented with bits of sea-shell, beads, and buttons . . . The same round basket-cap noticed before, is worn by the Klamath women [*b. c*, fig. 3], figures of different colors and patterns being worked into it. They tattoo the underlip and chin in the manner remarked at Eel river; the young girls in faint lines, which are deepened and widened as they become older, and in the married women are extended up above the corners of the mouth . . . The children are carried in baskets suspended from the head, after the manner shown in the sketch.

The original sketch to which this refers is reproduced in plate 15, figure 1. A picture of a "Young married Woman," also made at the forks of the Klamath and Trinity Rivers, October 6, 1851, is reproduced in plate 15, figure 2.

Continuing (p. 141):

The dress of the men consists, generally, of a pair of deer-skins with the hair on, stitched together. Sometimes, however, a noted hunter wears a couple of cougar skins, the long tails trailing behind him; and other again, on state occasions, display a breech-clout of several small skins, sewed into a belt or waistband . . . They are not as skilful in the preparation of dressed skins as the Oregon Indians, and the use of those dressed on both sides is mostly confined to the women.



FIG. 4.—Specimens collected by George Gibbs on the Klamath River, California.

a, food bowl of twined basketry, diameter $10\frac{1}{2}$ inches, depth $2\frac{1}{2}$ inches, U.S.N.M. no. 7568; *b*, food bowl of twined basketry, diameter $11\frac{1}{2}$ inches, depth 3 inches, U.S.N.M. no. 7563; *c*, cooking basket, diameter $9\frac{1}{4}$ inches, depth 4 inches, U.S.N.M. no. 7567; *d*, cooking basket, diameter $9\frac{1}{4}$ inches, depth $4\frac{1}{2}$ inches, U.S.N.M. no. 7553.

On the morning of October 9 the expedition left the mouth of the Trinity and continued up the valley of the Klamath. About 2 miles above the forks they arrived at—

the Hai-am-mu village, and visiting one of the lodges, found the inhabitants engaged in cooking and eating. The meal consisted of fish and acorn porridge, made by mixing the flour in a basket [*c*, *d*, fig. 4], in which the water is kept

boiling by means of hot stones. Of the acorn flour they likewise make a sort of bread, which they bake in the ashes. They had several spoons, very neatly made of bone or horn [a, b, fig. 5]. At this village there was a large fish-dam; a work exhibiting an extraordinary degree both of enterprise and skill . . . We camped opposite the high point which forms a land-mark from the Bald Hills, and which gives the name Bluff creek to a stream entering from the northwest, called by the Indians Otche-poh. Upon the other side of the river was an Indian village, the Sehe-perrh; the first belonging to the

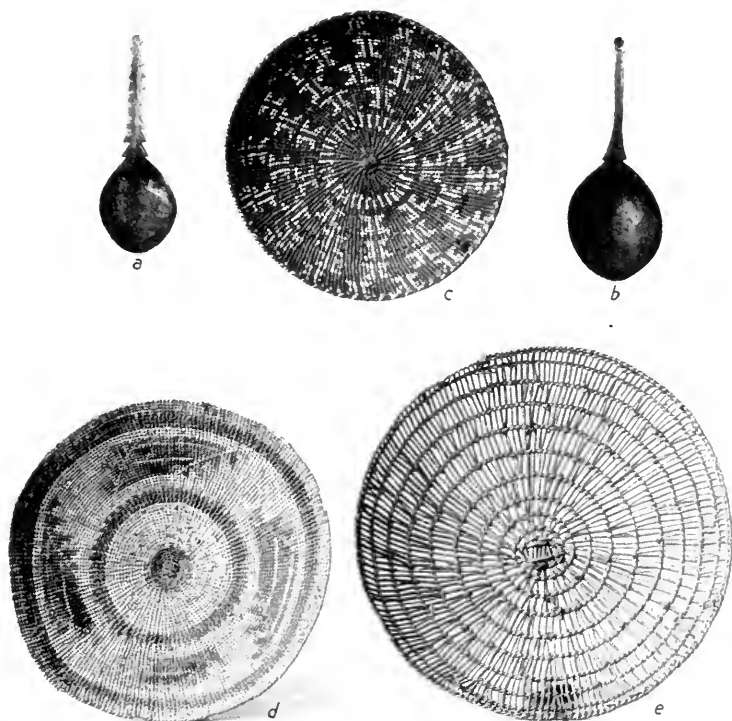


FIG. 5.—Specimens collected by George Gibbs on the Klamath River, California.

a, spoon made of elk antler, length $5\frac{1}{2}$ inches, U.S.N.M. no. 7510; *b*, spoon made of elk antler, length 6 inches, U.S.N.M. no. 7511; *c*, shallow food tray, diameter 7 inches, depth 2 inches, U.S.N.M. no. 7501; *d*, shallow food tray, diameter $10\frac{1}{2}$ inches, depth $1\frac{1}{2}$ inches, U.S.N.M. no. 7502; *e*, tray for draining liquid from food, diameter 12 inches, depth $2\frac{1}{2}$ inches, U.S.N.M. no. 7502.

tribe occupying the middle section of the river, and of which the Quoratem or Salmon river Indians may be considered as the type. [Pl. 16, fig. 1.]

The party encamped on the bank of the Klamath about 1 mile above the mouth of Salmon River and there remained from the afternoon of October 11 until the morning of the 13th. This was a rugged, mountainous region through which it was difficult to pass.

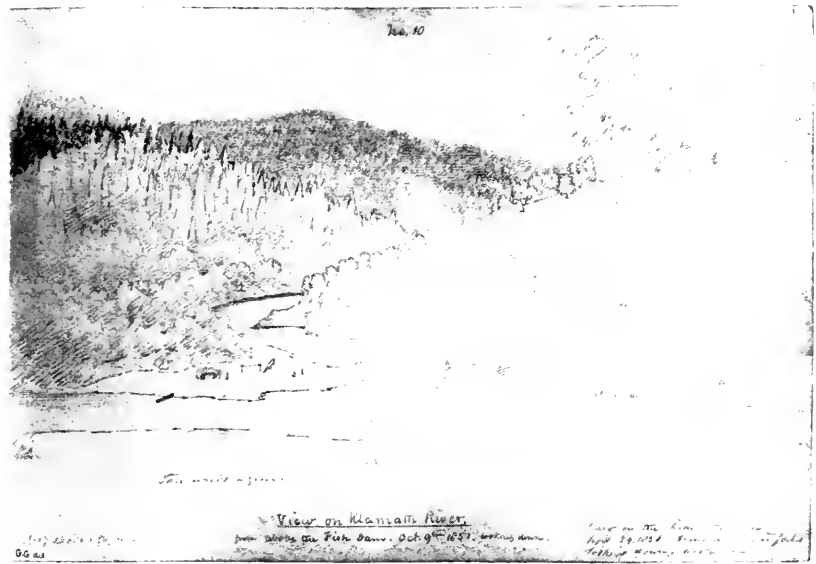
P. 150.—Salmon river, or as it is called by the Indians, the "Quoratam," is the largest of the affluents of the Klamath, with the exception of the Trinity . . . Upon the Klamath, both above and below the junction, are Indian villages of some size, prettily situated on high platforms of rock projecting over the water, and shaded by groves of oaks and bay trees; while below, the river, compressed in its channel, rushes boiling over rapids. The accompanying sketches were taken, one from near our camp, representing the Tish-ráwa village, and the Klamath, below the entrance of the Salmon [pl. 1]; the other from a mile higher up, showing the course of the Klamath through the mountains above the forks [pl. 16, fig. 2]. The tree on the right hand of the latter represents one of the signal or "telegraph" trees of the Klamath Indians. These, which are among the most conspicuous features of the scenery upon the river, occur near every village. They are always selected upon the edge of some hill, visible to a considerable distance in either direction. Two trees, one trimmed in the form of a cross, the other with merely a tuft on the top, represent each lodge; and in time of danger or of death, a fire kindled beneath them, informs the neighboring tribes of the necessity or misfortune of its occupants.

Scott's Valley, with "the snowy peak of Shasté lying to the south-east, towering above all," was reached on the afternoon of October 21. During the following days Gibbs, with other members of the party, made trips to the surrounding country to examine the valley and to contact the native tribes. On Sunday, October 26, he rode to Shasté Butte City, some 25 miles from the camp, and the next morning (p. 165):

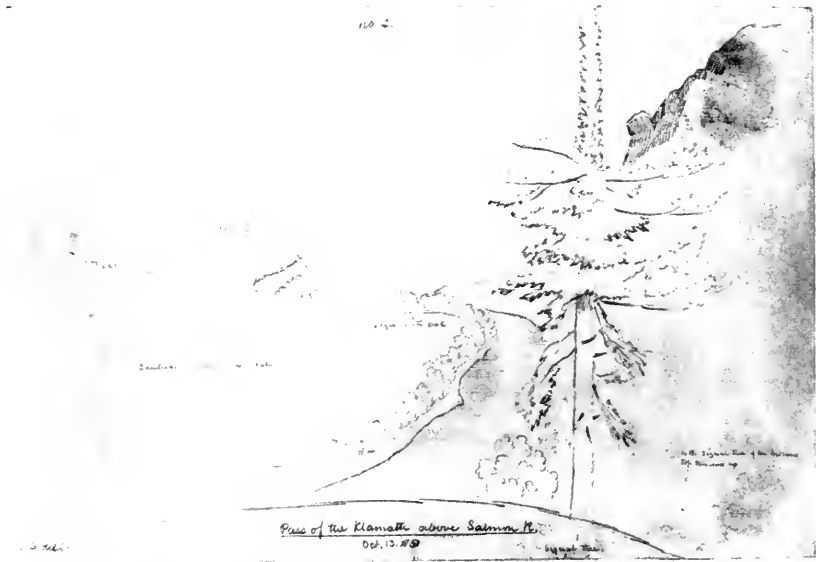
rode to the top of a range of hills about four miles distant, for the purpose of obtaining a view of the country. The prospect here was very extensive, commanding the northern and eastern portions of the plain, and extending south-easterly, to Mount Shaste, which was distant about thirty miles . . . From the same point of view we could see Mount Pitt, or more properly Pitt mountain, so called from the traps formerly dug near it, by the Indians; and the noted land-marks of the Oregon trail, the "Pilot Knob," on the Siskire range to the north, and the "Black or Little Butte," to the south. [Pl. 17.]

Members of the party, including Gibbs, started from Scott's valley camp about noon on November 6 to return to San Francisco. They passed over the same trail to their old camp on the Klamath, near the mouth of the Salmon, where they arrived on the 12th. There (p. 174):

several of our old acquaintances among the Indians visited us; and I succeeded in persuading a pretty girl, the chief's daughter, to sit for her portrait. The likeness was sufficiently good to be recognised, though it certainly did not flatter the very gentle and pleasing expression of her face . . . [pl. 15, fig. 3]. We found the Indians of the village which had been burnt down, rebuilding their houses for the winter. The style was very substantial, the huge poles requiring five or six men to lift. These lodges, it may be mentioned, are usually dismantled in summer, when the inhabitants live in temporary bush huts.



1. The Klamath above the fish dam, October 9, 1851.



2. The Klamath. Signal tree of the Indians on right. October 13, 1851.

VIEWS IN THE VALLEY OF THE KLAMATH



THE SHASTÉ BUTTE
From the base north-west of Shasté Valley

516 out

After encountering many difficulties and delays, Gibbs arrived at San Francisco December 28, 1851, "having been absent on the Expedition nearly five months."

The specimens collected by Gibbs on the Klamath River in California, which are now in the United States National Museum and many of which are shown in figures 3, 4, and 5, are believed to have been obtained by him during the autumn of 1851. Several of the pieces represent forms of objects mentioned specifically in his journal as being used by the Indians who were met during the journey up the valley of the Klamath, and these may have been collected at that time. All are excellent examples and were evidently chosen with care.

The bow, made of yew, is strengthened on the back by sinew which, although originally glued to the wood, has become detached. The cord, as shown in the photograph, is 34 inches in length.

The headband, *d*, figure 3, is described in the old list of specimens as "a ribbon for the hair," and is an unusual piece to have been preserved. If extended it would be about 20 feet in length, but it is arranged in 15 coils, held together at one place by an end being passed around the coils several times and fastened. The average width is $\frac{1}{8}$ inch, the average thickness about $\frac{1}{16}$ inch. As shown in the enlarged photograph, *c*, figure 3, it is formed of two twisted cords of vegetal fiber, each cord being made of two strands which are loosely twisted. The two cords of fiber are held together, parallel, by a light-colored grass, braided so as to allow the cords to remain separated. At irregular intervals the braided grass is omitted, thus allowing the two twisted cords to be exposed. There is a small loop at one end of the cords.

All baskets, basket hats, and trays are beautiful pieces and may be the oldest existing examples from that part of California.

The shallow tray, no. 7561, *d*, figure 5, is reenforced on the bottom by the attachment of pliable twigs or shoots, probably of the willow, which are bent to form circular bands, each band or ring being composed of two coils. Two such bands were used, one rather small and the other near the outer edge.

The two small spoons, *a*, *b*, figure 5, are typical examples and show the effect of much use.

MINUTES KEPT BY JOHN MCKEE IN NORTHWESTERN
CALIFORNIA, 1851

On October. 15, 1850, a letter was addressed to Redick McKee, Geo. W. Barbour, and O. M. Wozencraft, by the Acting Commissioner of Indian Affairs, Washington, which read in part ¹⁷ (p. 121) :

Gentlemen: I have the honor to enclose herewith a copy of a letter from the Secretary of the Interior, by which you will find that your functions and salaries as Indian agents are suspended; and that you are appointed, with the sanction of the President, commissioners "to hold treaties with various Indian tribes in the State of California," as provided in the Act of Congress, approved Sept. 30, 1850. Your commissions are also enclosed.

The three newly appointed commissioners met and entered into treaties with various tribes. They had worked together, but on May 15, 1851, wrote from Camp Barlow, San Joaquin River, to the Commissioner ¹⁸ (p. 224) :

We have now concluded, in view of the almost interminable extent of country to be traversed in carrying out our instructions, to cease as a board, and address ourselves to the work individually. We have made a temporary division of the State into three districts, for the purpose of negotiating treaties with the various tribes, upon the general plan submitted in our joint letter of 10th March. For our respective districts, lots were drawn to-day, and the northern fell to the writer (R. McKee,) the middle to O. M. Wozencraft, and the southern to George W. Barbour.

With the coming of immigrants, prospectors, and settlers, unrest and uncertainty developed among the Indians of northern California, and a general uprising was feared. As a result of the existing conditions it was deemed necessary for a commission to visit the various tribes in the endeavor to create friendship, to enter into treaties, and to set apart reservations where all could live in peace and security. Many of the scattered tribes, or groups, occupied secluded valleys, reached by narrow trails over mountains or through rocky ravines and often difficult to discover; nevertheless, the venture proved of much importance.

Redick McKee led the Expedition, and on July 29, 1851, wrote from San Francisco to Luke Lea, Commissioner of Indian Affairs, Washington, saying in part ¹⁹ (p. 128) :

¹⁷ *In Annual Report of the Commissioner of Indian Affairs . . . 1850. Washington, 1850.*

¹⁸ *In Annual Report of the Commissioner of Indian Affairs . . . 1851. Washington, 1851.*

¹⁹ *The journal or Minutes kept by John McKee, secretary, on the expedition from Sonoma, through northern California, and many letters pertaining to the*

At present I can form no satisfactory estimate of the amount of appropriations our treaties will require . . . The largest estimate will fall below the cost of a *California Indian year*, if one should unhappily become general . . . I am anxious to get off, so as, if possible, to make the journey before the rainy season sets in. I propose taking the Clear Lake Indians on my route, who are said to number three or four thousand, and will endeavor to make pacific arrangements with them before passing over the coast range. On the Klamath and Trinity rivers, from all the accounts I have received, I shall find large bodies of the largest, wildest, most intelligent, and warlike Indians in California.

The commission, accompanied by an escort of 36 dragoons under command of Maj. W. W. Wessells, United States Army, left Sonoma August 11, 1851. As stated in the journal (p. 134): "Agent McKee moved with his escort from Sonoma, at 8 o'clock a. m., and the command is now encamped 19 7/10 miles up the Sonoma valley, on the Russian river valley trail. Mr. George Gibbs has been employed as Chinook interpreter . . ." ²⁰

Two days later, August 13, the party left the Sonoma valley and followed a trail on the west side of Russian River, and that night encamped "five or six miles below the first cañon, or defile, through which the stream flows." The next day the commission was joined by Gen. J. M. Estelle and staff, of the 2d division of the California militia, who had been sent by the Governor to assist in effecting treaties with the Indians residing near Clear Lake and Russian River.

On the night of August 16 the entire party camped on the bank of Russian River, then moved on to (p. 136):

Camp Lupiyuma, near Clear lake, August 17, 1851.—R. McKee and party, composed of secretary, and Gibbs as interpreter, with a sufficient number of pack-mules to transport provisions and such presents as are designed for the Indians; also ten head of cattle, with a detachment of ten dragoons in charge of Major Wessells as an escort, all under the guidance of two Indian guides,

undertaking, were included in the Report of the Secretary of the Interior . . . March 17, 1853. Special Session, Senate Ex. Doc. No. 4. The following quotations, unless otherwise stated, are from that document.

²⁰ McKee sent a lengthy letter to the Commissioner of Indian Affairs dated "Camp at Big Bend of Eel River, September 12, 1851," in which he said (p. 181): "At Sonoma I was fortunate in securing the services of George Gibbs, formerly of New York, and recently attached to the Indian commission in Oregon. He is acquainted with the Tchinnook (Chinook) language, and the *jargon* spoken by all the tribes on the borders of Oregon and California. He is, moreover, a practical topographical engineer; has kept a journal of our entire route, and will furnish me, I hope, in time for my final report, a correct map and reconnaissance of the trail from Sonoma, showing the exact position of all the important rivers, lakes, mountains and valleys, together with a synopsis of the various dialects of the tribes we have met."

left the main camp at an early hour this morning, and commenced ascending the mountains dividing the Russian river and Clear Lake valleys, following a narrow, precipitous trail leading in many places through a dense forest, with oak and chemisall undergrowth . . . We are encamped upon the table-lands immediately adjoining the lake. Several Indians have visited camp this evening, and we expect to have several chiefs in council to-morrow.

On the morning of the 18th "according to agreement a number of the chiefs and braves of the Clear Lake Indians" met the commission in council. Much of interest and importance transpired during the succeeding hours. The Council again convened on Tuesday afternoon, August 19, when McKee explained to the Indians the nature of the proposed treaty, and stated that he would give them, in the name of the President, "all of the Clear Lake valley proper, upon condition they would all live in it peaceably, and agree that all other tribes the President may send among them to live should be received as brothers, &c." To this the Indians agreed.

The party returned to the main encampment on Russian River and soon continued northward. During August 25, they crossed the mountains between the Russian and Eel Rivers and that night camped in a valley near an old Indian village. The Indians were "entirely nude and very wild." Many Indians appeared at the camp the following morning, and the commissioner explained the nature of the treaties made with the Indians at Clear Lake and Russian River, after which there was a mutual understanding for peace.

The expedition continued through the mountains, but advanced slowly over unknown trails. They left camp early on August 29 but were soon forced to stop in a cañon, a place where sufficient water could be obtained for the animals. During the day 15 or 16 Indian men, all entirely naked, visited the camp. From them it was learned that many Indians were living in "a long valley on the headwaters of the middle fork of Eel river." The party had been unable to discover the valley, although they had spent several days in hunting for it. The Indians called the valley Ba-tim-da-kia.

During September 5 and 6, the expedition rested at Camp Redwood, on the South Fork of Eel River.

On September 10, the camp was at "Big Bend of Eel river," where the party remained several days. Gibbs had, as always, been active in obtaining information concerning the Indians, and as mentioned in the journal (p. 151): "Some words, relating to sensible objects, have been obtained by Mr. Gibbs. The names of tribes could not be ascertained, nor their numbers. But he has learned that all the Indians around Humboldt bay, and as far up Eel river as Van Dusen's fork, say fourteen miles, speak the same language. Above the forks a

different dialect is spoken, but so as to be understood by the different tribes." And at the same camp two days later "about a dozen naked Indians hanging around camp were supplied with food and some clothing."

The following morning, September 13, Gibbs, with two other members of the party, left camp to "proceed in a canoe down Eel river to its mouth." This was to enable him to explore the country south of the river, and to meet the Indian inhabitants of the region in the endeavor to have them visit the camp. Gibbs returned to the main camp on the evening of September 14, after having reached the mouth of the river, and stopping at 10 or 12 Indian rancherias on the banks of the stream where they distributed presents. That same evening "the express despatched to Port Trinidad returned . . . with despatches from the Indian department at Washington."

"Camp of Humboldt City, September 15, 1851.—Finding it impossible to collect the Indians, or to hold proper communication with them, R. McKee moved camp with the escort this morning, and encamped at this place, after a march of twelve miles . . ." On the following day they crossed Eel River at low tide and moved a few miles to Bucksport. An entry in the journal that day states (p. 154): "The bands of Indians living upon Eel river have no permanent place of residence, but move from river to mountain and from mountain to river, as the season for fishing and gathering nuts and berries arrives; and among the different bands, though not at actual war, no friendly intercourse exists."

Soon they resumed their journey northward, encountering many Indians as well as white settlers, and so approached one of the most important centers. They arrived at (p. 156):

Bloody Camp, September 27, 1851, three miles from the junction of the Klamath rivers.—Reached this camp, upon the top of a mountain, after a very tedious march of twelve miles. Several Indians were seen upon the trail to-day, but fled to the woods when approached. Fine grass and water on this mountain. The agent has gone forward this morning to examine the pasture, &c., near the junction, with a view to the removal of our camp to a suitable place for a treaty ground, if one can be found. The country around the junction is a wild mountainous region, entirely unfit for cultivation, and indeed can scarcely be travelled by pack-mules. The Indians are said to be numerous, and subsist chiefly on the salmon and salmon trout, which the rivers afford in great abundance, and on the berries, nuts, &c., obtained on the mountain sides. Deer, elk, bear, &c., are quite plenty, but the Indians kill but few, as their only arm is the bow and arrow.

Two days later, September 29, McKee accompanied by part of his guard, established a camp at the junction of Klamath and Trinity

Rivers where they remained until October 9. Many Indians gathered near the camp (p. 157) :

The Indians here are a very fine-looking race, low in stature, with smooth, regular features. The men are nearly nude, and never seen without the bow and quiver of arrows, exhibiting considerable skill in their construction. The women wear petticoats of deer-skin, dressed and ornamented with tassels, beads, shells, &c. Some of them are very handsomely made. Strings of beads and shells are also worn about the neck, and ornaments of every description are highly prized.²¹

On October 6, a treaty was concluded with the many groups of Indians who had gathered for that purpose at the junction of the Klamath and Trinity Rivers, and that night (p. 162) : "Presents of blankets, shirts, pants, beads, shawls, handkerchiefs, &c., &c., were distributed by the light of large fires; after which the Indians all separated for the night, well pleased." Among the bands present that day was the "Wetch-peck band" of which Mec-ug-gra was chief. (Pl. 18.)

On October 9, the party moved from the vicinity of the junction of Klamath and Trinity Rivers, crossed the Klamath at Durkee's ferry, and established camp near Bluff Creek. During the day they traversed a rough mountain trail. A sketch made at that time shows a small Indian encampment in the bend of the river.

The Indians near Salmon River speak a different dialect from those below them.

Camp Cor-a-tem, near mouth of Salmon river, October 12, 1851.—R. McKee remained at this camp to meet the Indians of this neighborhood as agreed. At 10 o'clock about 150 men and women were assembled. Each band arranged

²¹ Quantities of trade beads were distributed among the Indians of California. They were received from several sources, and the following letter will tell where some were obtained (p. 360) : Letter from P. B. Reading to Luke Lea, Indian Commissioner—

Washington, September 10, 1852.

"SIR: Please notice below a memorandum of articles which I would recommend to be purchased for presents to be distributed among the Indians in California. It will be well to make the purchases in New York, as it is quite uncertain if Mr. Beale, the superintendent, could find the articles in California :

Small white porcelain beads.....	\$4,500
Small black porcelain beads.....	2,000
Small red porcelain beads.....	3,000
Large glass beads, assorted.....	2,000
Turkey red prints.....	2,500
Gay-colored shawls	1,500

15,500

"It will be necessary that the packages be made up to the weight of about 200 lbs., and well secured in oilcloth coverings, in order to prevent damage to contents, as the present is the rainy season."



Young Weit-spek Chief
Yinnig Oren -

YOUNG CHIEF OF THE WEIT-SPEK TRIBE, PROBABLY MEC-UG-GRA

Drawn by Capt. Seth Eastman, from original sketch by George Gibbs,
October 1851.

separately, communicating with them through Mr. C. W. Durkee, and he through the Wetchpeck Indian from the junction of Klamath and Trinity . . .

The number of Indians living near this camp, around the mouth of Salmon river, is about 225 souls, all told. They compare favorably in size and appearance, and intelligence, with the Indians below; speak a different dialect, though they intermarry with them. Their houses are built of slabs split out from redwood timber, in which a family of ten or fifteen will reside, relying principally upon fish for a subsistence.

The following day, October 13, the party was in "Camp on Klamath river, 12 miles above mouth of Salmon river." The trail over which they passed that day was difficult and dangerous, and "several of our animals fell from the trail and rolled down the mountain, but were recovered and brought into camp." Gibbs made another sketch of the rugged mountain scenery.

"*Camp in Scott's valley, October 21, 1851* . . . Our route to-day led up the Klamath river to the north of Scott's river; thence up Scott's river to Scott's bar, where a large number of miners have been and are at work; thence crossing Scott's river, and over a high, steep mountain into this valley . . ." The party remained in the valley several days, during which time the surrounding country was examined. On the 24th "Messrs. Gibbs, Kelsey, and Woods have been sent out to explore and examine this valley, and adjacent hills and mountains, relative to its adaptation for an Indian reservation." Two days later, October 26, "Mr. George Gibbs was despatched to Shasta plains to examine that part of the country."

"*Camp in Scott's valley, October 27, 1851*.—This is the day appointed for the Indians in Shasta and Scott's valleys, and on Scott's river, to assemble at this camp . . . The citizens of Shasta Butte city assembled."²²

Remained in Scott's valley until November 6, when they "commenced the march for the coast by the same trail we came over from Durkee's ferry." Continued on through the mountains and on November 11 "crossed to the east side of the Klamath at an Indian rancheria, swimming our animals—no accidents."

"*November 12, 1851*.—Detained some time this morning getting our mules from the mountain, and crossing our goods over in canoes: swimming the mules over, they became alarmed, and two were drowned. This to us is a serious loss . . . Started at 10 o'clock, and reached our old camp 'Coratem,' near the mouth of Salmon river, at 4." And the next morning "Mr. Gibbs and myself took a canoe and three Indians this morning and descended the river, passing many

²² On July 30, 1852, McKee wrote to Luke Lea, Commissioner of Indian Affairs, Washington, and referred to happenings "in the neighborhood of *Yraka* (late Shasta Butte city)." (P. 353.)

dangerous ripples or rapids, and at 4 o'clock reached Durkee's ferry, mouth of Trinity river."

The expedition was disbanded and Gibbs went to San Francisco.

Quotations from two letters written by Redick McKee, to Luke Lea, Commissioner of Indian Affairs, Washington, will shed light on subsequent events (pp. 294-297):

San Francisco, March 1, 1852.

... Since I wrote I have received from Mr. George Gibbs his report, or journal, of the expedition to northern California, accompanied by a very beautiful map of the country traversed, and sundry vocabularies of the languages spoken by the tribes we visited. These I design sending to you by the mail which takes this; but our friend, General S. D. King, of the land survey department, is making a copy of the map, and the Senate Committee on Indian Affairs desires me to afford them a reading of Mr. Gibb's views as to the reservations made for the Indians, at a meeting appointed for the 4th instant ...

P. S. Mr. Gibbs having forwarded some sketches to Mr. Schoolcraft by the last mail, I will, with this, send the vocabularies.

The second letter reads in part:

San Francisco, March 13, 1852.

SIR: My last despatch was dated 1st instant, and accompanied a sealed package of vocabularies, prepared by Mr. George Gibbs. I have deposited in the post office, to go with this letter, Mr. Gibb's map of my route through northern California, and his manuscript journal of the expedition. This journal, the map, and the sketches forwarded by last steamer to Mr. Schoolcraft, will, I hope, be *neatly and carefully published*. They will throw some additional light upon a part of this State, not previously explored. On this subject, I enclose letters from Mr. Gibbs to the honorable Senators Hamilton Fish and Truman Smith, and to H. R. Schoolcraft, esq., which you will please read, and then deliver.

It is now possible, after the lapse of many years, to present the sketches "neatly and carefully published," together with others which were made by Gibbs before he joined McKee on the journey into northwestern California.

During subsequent years, until his departure from the Pacific coast late in 1860, Gibbs' interest in the Indians continued. He made vocabularies among the native tribes scattered over a wide region, and gathered ethnographical material in California, Oregon, and Washington, on Puget Sound and far up the Columbia. As such material was at that time so plentiful, it is evident he selected choice specimens to be carried, or sent, to his home in New York. If all the material thus collected could be brought together, it would prove of special interest as representing the work of tribes then living in their primitive state, maintaining manners and customs that had been followed and practiced for generations, but which were soon to be lost or changed through contact with those who came to claim and occupy the country.



SMITHSONIAN MISCELLANEOUS COLLECTIONS
VOLUME 97, NUMBER 9

A NEW NUTHATCH FROM YUNNAN

BY
H. G. DEIGNAN
Division of Birds, U. S. National Museum



(PUBLICATION 3486)

CITY OF WASHINGTON
PUBLISHED BY THE SMITHSONIAN INSTITUTION
OCTOBER 10, 1938

SMITHSONIAN MISCELLANEOUS COLLECTIONS
VOLUME 97, NUMBER 9

A NEW NUTHATCH FROM YUNNAN

BY
H. G. DEIGNAN
Division of Birds, U. S. National Museum



(PUBLICATION 3486)

CITY OF WASHINGTON
PUBLISHED BY THE SMITHSONIAN INSTITUTION
OCTOBER 10, 1938

The Lord Baltimore Press
BALTIMORE, MD., U. S. A.

A NEW NUTHATCH FROM YUNNAN

By H. G. DEIGNAN

Division of Birds, U. S. National Museum

A series of 26 specimens of the giant nuthatch, representing the material in the United States National Museum, the American Museum of Natural History, and the Academy of Natural Sciences, Philadelphia, shows that the bird of northwestern Yunnan is quite distinct from *magna*, based on specimens from Karen-ni. For the new form I propose the name

SITTA MAGNA LIGEA, n. subsp.

Type.—Adult male, U.S.N.M. no. 297271; collected at Likiang, northwestern Yunnan, 8,200 feet, August 1923, by Dr. Joseph F. Rock.

Diagnosis.—Readily distinguished from *Sitta magna magna* by its markedly shorter and laterally slenderer bill, although not separable by color characters or other measurements. The culmens of nine males from northwestern Siam and the Shan States measure (from the base of the rhamphotheca) 30.3 to 32.5 mm (average: 31.4 mm); of eight females from the same localities, 29.5 to 32.5 mm (average: 31 mm). On the other hand, the culmens of four males from the mountains of Likiang measure 26 to 28.5 mm (average: 27.1 mm). The difference in the "heaviness" of the bill is scarcely to be shown in figures, but is very obvious to the eye.

Range.—Northwestern Yunnan: the Likiang mountains, 8,200 to 10,000 feet; Yung-pei.

Remarks.—I have not seen topotypical *magna*, but feel justified in considering Siamese specimens, taken about 50 miles east of Karen-ni, to belong to that form, especially since they agree perfectly with Shan States examples which British authors have held to be identical with Karen-ni birds.

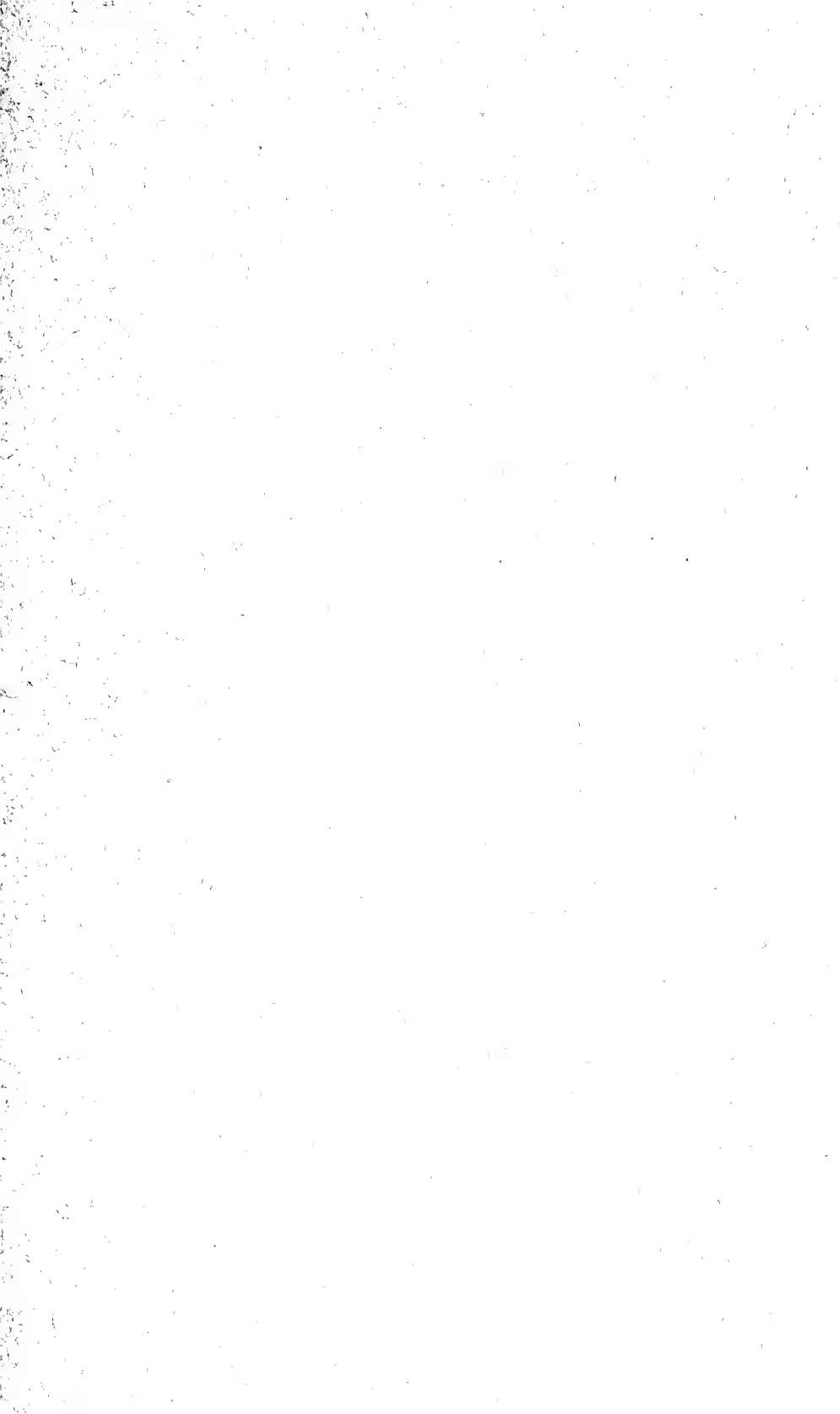
Two Shan birds, whose measurements are not included above, are not fully mature, as is indicated by the texture of the plumage. In these specimens, the bill is as short as in the Likiang examples, but at the same time as thick laterally as in fully adult Shan specimens, a combination which gives it a peculiarly blunt appearance for a nuthatch.

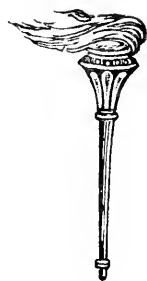
The sexes of this species are easily separable in series. The male has the dark markings of the head wholly glossy blue-black; in the female they are dull black or black washed with gray, with a tendency to gloss only on the shoulders. In the male the mantle is slaty-blue; in the female paler slaty and much less suffused with blue. The female has the underparts pale gray, more or less suffused throughout with buff or pale chestnut; the male has the same parts wholly a soft blue-gray, with buffy suffusion confined to the lower abdomen. The chin and throat are white in either sex, but in the female they are faintly washed with buff.

The "Fauna of British India" describes the upper plumage simply as "slaty-blue," and fails to mention one of the most striking characters of the species. Actually, the whole portion of the head, neck, and upper back included between the broad black stripes is quite different from the mantle, the front and crown being a soft blue-gray, changing gradually to a still paler gray upon the nape and upper back, which is sharply defined from the color of the remaining upperparts. In the female the light portion is very faintly suffused with buff, and, because the adjacent colors are less contrasting, is slightly less conspicuous than in the male.

The front and crown in either sex may have more or less black streaking in the gray. In the series before me, these parts vary individually from immaculate gray to almost solid black.

My thanks are due to John T. Zimmer, who has kindly sent me the Burmese material from the Rothschild collection, and to R. M. de Schauensee, who has lent me the Yung-pei specimen of *ligea*, as well as his valuable series of *magna* from Siam.





SMITHSONIAN MISCELLANEOUS COLLECTIONS
VOLUME 97, NUMBER 10

FOURTH CONTRIBUTION
TO NOMENCLATURE OF CAMBRIAN
FOSSILS

BY

CHARLES ELMER RESSER

Curator, Division of Invertebrate Paleontology,
U. S. National Museum



(PUBLICATION 3487)

CITY OF WASHINGTON
PUBLISHED BY THE SMITHSONIAN INSTITUTION
DECEMBER 17, 1938

SMITHSONIAN MISCELLANEOUS COLLECTIONS
VOLUME 97, NUMBER 10

FOURTH CONTRIBUTION
TO NOMENCLATURE OF CAMBRIAN
FOSSILS

BY

CHARLES ELMER RESSER

Curator, Division of Invertebrate Paleontology,
U. S. National Museum



(PUBLICATION 3487)

CITY OF WASHINGTON
PUBLISHED BY THE SMITHSONIAN INSTITUTION
DECEMBER 17, 1938

The Lord Baltimore Press
BALTIMORE, MD., U. S. A.

FOURTH CONTRIBUTION TO NOMENCLATURE OF CAMBRIAN FOSSILS

By CHARLES ELMER RESSER

*Curator, Division of Invertebrate Paleontology,
U. S. National Museum*

This is the fourth paper in a series dealing with nomenclatural changes necessary for Cambrian fossil species.¹ In this paper non-trilobitic and non-American species are included. It was hoped all necessary changes in sight could go in this fourth contribution, but that proved to be impossible. Several descriptive papers now in press or nearing completion involve previously described species, and thus make additional nomenclatural changes. Moreover, it is the practice to withhold references of species to new genera where undescribed species are in hand which will make better genotypes. Needed changes are also withheld in instances where someone is known to be at work on the faunas which contain improperly named species.

The nontrilobitic species are discussed first, grouped according to classes. The trilobites are again placed in alphabetical order according to genera.

BRACHIOPODA

PATERINIDAE Schuchert

MICROMITRA Meek, 1873

Micromitra minutissima (Hall and Whitfield)

Kutorgina minutissima HALL and WHITFIELD, U. S. Geol. Expl. 40th Par., vol. 4, pt. 2, p. 207, pl. 1, figs. 11, 12, 1877.

Kutorgina sculptilis WALCOTT (part), U. S. Geol. Surv. Mon. 8, p. 20, pl. 1, fig. 7b; pl. 9, fig. 7, 1884.

Micromitra sculptilis WALCOTT (part), idem, 51, p. 341, pl. 3, figs. 5b, c, 1912.

The Nevada form is distinct from *M. sculptilis* of Montana in having coarser ribs. For this reason the old species name is restored.

¹ Resser, Charles Elmer, Nomenclature of some Cambrian trilobites, Smithsonian Misc. Coll., vol. 93, no. 5, Feb. 14, 1935; Second contribution to nomenclature of Cambrian trilobites, idem, vol. 95, no. 4, Apr. 1, 1936; Third contribution to nomenclature of Cambrian trilobites, idem, vol. 95, no. 22, Apr. 5, 1937.

Middle Cambrian, Eldorado; (loc. 58) east side New York and Secret Canyons, Eureka District, Nevada.

Cotypes.—U.S.N.M. no. 24551a, b.

***Micromitra burgessensis*, n. sp.**

Micromitra (Iphidella) pannula WALCOTT, Smithsonian Misc. Coll., vol. 67, no. 9, p. 481, pl. 106, fig. 16, 1924.

This species conforms in every respect to the characteristics of *Micromitra* even though only one valve has been found. The growth lines are pronounced and are wavy and close together. Ribbing is well developed, and the ribs have the usual irregularities. Because of the crinkly growth lines and particularly because of the preservation of long slender spines which extend far beyond the margin, this shell was regarded as the same as *I. pulchra*. However, a glance at the illustrations shows that the two forms are quite different and that *pulchra* is a true *Iphidella*.

Middle Cambrian, Burgess; (loc. 35k) Burgess Pass, near Field, British Columbia.

Holotype.—U.S.N.M. no. 69646.

PATERINA Beecher, 1891

***Paterina troyensis*, n. sp.**

Scenella retusa WALCOTT (part), U. S. Geol. Surv. Bull. 30, p. 120, pl. 12, fig. 3a, 1886 (not fig. 3 = *Stenothecoides*).

The specimen doubtfully referred to *Scenella retusa* by Walcott is a brachiopod belonging to *Paterina*. It is a small form only 1.5 mm long and 1 mm high. About halfway back a depression follows the position of an ordinary growth line, but this is regarded as an accidental feature. The shell appears to be nearly smooth, but this may be due to imperfect preservation.

Lower Cambrian, Schodack; (loc. 27) Troy, New York.

Holotype.—U.S.N.M. no. 15369.

***Paterina zenobia* (Walcott)**

Micromitra (Paterina) stissingensis? WALCOTT (part), U. S. Geol. Surv. Mon. 51, p. 353, pl. 3, fig. 1e, 1912.

Micromitra (Paterina) stissingensis ora WALCOTT, idem, p. 354, 1912.

Micromitra zenobia WALCOTT, idem, p. 342, text fig. 23, 1912; Smithsonian Misc. Coll., vol. 67, no. 9, p. 481, pl. 106, figs. 1-7, 1924.

Middle Cambrian, Burgess; (loc. 35k) Burgess Pass, (locs. 61j, 35k') West slope Mount Field; (loc. 14s) Mount Stephen near Field, British Columbia.

Holotype.—U.S.N.M. no. 58311; plesiotypes, nos. 50907, 51483, 69631-7.

IPHIDELLA Walcott, 1905

Iphidella fieldensis, n. sp.

Micromitra (Iphidella) pannula WALCOTT (part), Canadian Alpine Journ., vol. 1, no. 2, pl. 1, fig. 1, 1908; U. S. Geol. Surv. Mon. 51, p. 361, pl. 14, fig. 1r, 1912.

This species was confused with *I. pannula* but there is little resemblance. *I. fieldensis* is characterized by a fairly well developed diamond pattern on the older part of the shell, which is more and more obscured toward the margins by increase in prominence of the wavy growth lines.

Middle Cambrian, Stephen; (loc. 14s) Mount Stephen; (loc. 35k) Burgess Pass, near Field, British Columbia.

Holotype.—Walker Mus., Toronto.

Iphidella pulchra, n. sp.

Micromitra (Iphidella) pannula WALCOTT, Research in China, vol. 3, Carnegie Inst. Publ. 54, pl. 1, fig. 13, 1913; Smithsonian Misc. Coll., vol. 67, no. 9, p. 482, pl. 106, fig. 17, 1924.

This is a very beautiful brachiopod. Well-preserved specimens show "spines" extending far beyond the margins of the shells. *I. pulchra* carries the diamond pattern to its extreme development. Very large specimens show the pattern interrupted somewhat in the outer part of the shell by rather heavy growth lines.

Middle Cambrian, Burgess; (loc. 35k) Burgess Pass; (loc. 14s) Mount Stephen, near Field, British Columbia.

Holotype.—U.S.N.M. no. 59801.

OBOLIDAE King

LINGULELLA Salter, 1866

The family Obolidae includes many brachiopod genera, chief of which in Cambrian strata are *Obolus* and *Lingulella*. Each contains many species, and to both genera are assigned a number of subgenera. Discrimination of oboloid brachiopods is an inexact procedure at present because no one has yet determined what the characteristics essential for classification may be. Relative size and shape, and sometimes shell ornamentation, are the only usable criteria.

Proper generic names are not available for many Cambrian species. It is evident that most, if not all, of the subgenera in *Obolus* and *Lingulella* are valid genera, but these two names themselves are in question. One thing is certain, namely, that *Obolus* must be confined to post-Cambrian species. *Lingulella* is founded on *L. davisi* McCoy.

also a post-Cambrian brachiopod. Unfortunately the specimens of *L. davisii* are poorly preserved; consequently it is difficult to determine whether Cambrian forms are congeneric.

Distinctions of generic rank between the Cambrian species referred to *Obolus* and those placed in *Lingulella* seem to be wanting. In fact the assignment of species to these genera has been on the basis of shape alone, the wide forms being called *Obolus*. Pending revision of these brachiopods, Cambrian species which formerly would have been placed partly in *Obolus* and partly in *Lingulella* are preferably referred to *Lingulella*.

***Lingulella bridgei*, n. sp.**

Lingulepis acutangula BRIDGE (part), U. S. Geol. Surv. Prof. Paper 186-M, p. 244, pl. 68, figs. 4, 5, 1937.

The stratigraphic position of the sandstone containing this species has not yet been determined with certainty.

This is a large form for which reason Bridge confused it with *Lingulepis acutangula*. However, it lacks the necessary restriction of the ventral valve at the apical end, tapering too slowly and evenly to be referred to *Lingulepis*.

The ventral valve figured by Bridge is broken away on the sides toward the apex, thus causing it to approach the form of *Lingulepis*. A smaller, more perfect ventral valve shows the true proportions of the shell, and while the valve comes to a rather sharp point, the margins approach the apex as slightly convex lines. The dorsal valve figured by Bridge is fairly complete but evidently somewhat flattened.

L. bridgei has the usual shell composition. A ventral valve about 15 mm long is 10 mm wide.

Upper Cambrian, Lion Mountain ?; $\frac{1}{4}$ mile east of Sandy, Blanco County, Texas.

Cotypes.—U.S.N.M. no. 93009.

***Lingulella burnetensis*, n. sp.**

Obolus matinalis WALCOTT (part), U. S. Geol. Surv. Mon. 51, p. 400, pl. 8, figs. 1a, b, 1912; BRIDGE (part), in Sellards, Adkins, and Plummer, Univ. Texas Bull. 3232, pl. 2, fig. 14, 1932.

This is a rather wide form, which is perhaps the reason for its reference to *O. matinalis* in spite of its larger size. There is some question as to the specific identity of the specimens from the two localities. Since the holotype is in sandstone it may come from the Lion Mountain sandstone member. The other specimens (loc. 67) are clearly in the *Aphelaspis* zone.

This species is characterized by its broad shape. The ventral valve has a sharp apex but widens rapidly, so that the holotype is about 14 mm long and 12 mm wide.

Upper Cambrian, Cap Mountain; (locs. 67, 67c) near the top of Potatotop, 7 miles northwest of Burnet, Texas.

Holotype.—U.S.N.M. no. 52420; paratype, no. 52419.

***Lingulella alia*, n. sp.**

Obolus matinalis WALCOTT (part), U. S. Geol. Surv. Mon. 51, p. 400, pl. 8, fig. 1k, 1912; BRIDGE (part), in Sellards, Adkins, and Plummer, Univ. Texas Bull. 3232, pl. 2, fig. 15, 1932.

This is a smaller brachiopod than the Cap Mountain species, *L. burnetensis*. Both valves are very wide, the holotype dorsal valve being about 9 mm long and 9 mm wide. Even though the ventral valve appears to be less wide, measurements show but little difference between length and width.

Upper Cambrian, Wilberns; (loc. 71) Cold Creek Canyon, San Saba County, and (loc. 14c) Baldwin's Ranch, Cold Creek, Llano County, Texas.

Holotype.—U.S.N.M. no. 51566.

***Lingulella monticola*, n. sp.**

Lingulella perattenuata WALCOTT (part), U. S. Geol. Surv. Mon. 51, p. 523, pl. 21, fig. 1e, 1912.

This small, neat form was referred by Walcott to *L. perattenuata*. The ventral valve is about 6 mm long and 3.5 mm wide, and the rate of taper is nearly rapid enough to warrant reference to *Lingulepis*. Otherwise the species conforms to the norm for the genus. This form is more slender than the older species, *L. longula*.

Upper Cambrian, Cap Mountain (Lion Mountain member?); (loc. 67c) Potatotop, 7 miles northwest of Burnet, Texas.

Holotype.—U.S.N.M. no. 27424.

***Lingulella longula*, n. sp.**

Lingulella perattenuata WALCOTT (part), U. S. Geol. Surv. Mon. 51, p. 523, pl. 21, figs. 1f, g, 1912.

L. perattenuata is thus far confined to the Black Hills and the name must be restricted to Whitfield's specimens. Unfortunately they do not warrant the precise drawings Walcott presents. The form from the Middle Cambrian of the Grand Canyon is an undescribed species. The specimens in sandstone from locality 70 also represent a new species, but since most of the material from that

locality belongs to the Wilberns formation, the horizon of the sandstone is in question.

L. longula is associated with *Obolus sinoc*, from which its elongate shape readily distinguishes it. Compared to *L. peraltenuata*, *L. longula* averages much smaller in size and is more slender. Only dorsal valves are figured by Walcott but ventral valves are present in the collection. The shell has the usual growth lines well marked. The smaller type specimen is about 5 mm long and 3 mm wide.

Upper Cambrian, Hickory; (loc. 68y) Packsaddle Mountain, 11 miles southeast of Llano, Texas.

Cotypes.—U.S.N.M. no. 27422.

***Lingulella hilli*, n. sp.**

Obolus (*Lingulella*) *acutangulus* WALCOTT, Proc. U. S. Nat. Mus., vol. 21, p. 392, pl. 27, fig. 6; pl. 28, figs. 1, 2, 1898.

Lingulella acutangula WALCOTT (part), U. S. Geol. Surv. Mon. 51, p. 474, pl. 17, figs. 1a, b, c, f, h, j, 1912.

Lingulella arguta BRIDGE, U. S. Geol. Surv. Prof. Paper 186-M, p. 245, 1937.

Bridge recently pointed out that Walcott's *L. acutangula* is not related to *Lingulepis acutangula* of Roemer with which it was identified, and further suggested that this brachiopod is *L. arguta*. However, Bridge failed to note that several species from different horizons were included by Walcott in *L. arguta*.

Walcott's original identification of Roemer's species was based on the Hickory sandstone specimens described here as *L. hilli*. Subsequently (1912) Walcott added Wilberns specimens which belong to a much larger species. The matrix of *L. hilli* is a black rock, consisting mainly of hematite in which there are scattered poorly rounded grains of clear quartz. The brachiopods are not compressed and many specimens retain a limy shell. This material was collected by R. T. Hill about 1885 from an undetermined locality in Llano County. When the shell is dissolved, many specimens show the internal features, which explains Walcott's choice of them to illustrate the species even though the locality is unknown.

L. hilli varies in size, averaging about 7 mm long and 4.5 mm wide for the ventral valve, with the dorsal relatively shorter. The other features are those usually characterizing *Lingulella* species.

L. hilli is larger and wider than *L. arguta* from Nevada.

Upper Cambrian, Hickory; Llano County, Texas.

Cotypes.—U.S.N.M. no. 35240.

Lingulella texana Walcott

Obolus sinoc WALCOTT (part), U. S. Geol. Surv. Mon. 51, p. 415, pl. 26, figs. 2-2d, 1912.

Lingulella texana WALCOTT, Smithsonian Misc. Coll., vol. 53, no. 3, p. 71, pl. 8, fig. 5, 1908; U. S. Geol. Surv. Mon. 51, p. 535, pl. 49, figs. 3, 3a.

Walcott's description stresses the radiating striae on the "outer surface" of the shell as the diagnostic feature. When it is remembered that the ribbing of a *Lingulella* shell is exposed only by exfoliation of one or more layers, this species loses its distinctive feature. This explains why specimens which retained the outer shell layers were referred to *Obolus sinoc*.

Upper Cambrian, Wilberns; (loc. 70) Baldy Mountain, 8 miles northwest of Burnet, and (loc. 69) Honey Creek, 8 miles southeast of Llano, Texas.

Holotype.—U.S.N.M. no. 51806; paratype, no. 51805; plesiotypes, no. 51627.

Lingulella lochmanae, n. sp.

Obolus (Lingulella) acutangulus WALCOTT (part), U. S. Geol. Surv. Mon. 51, p. 474, pl. 17, figs. 1, d, e, g, i, k, m-o, 1912.

Lingulella arguta LOCHMAN, Journ. Pal., vol. 12, no. 1, p. 85, pl. 18, figs. 17-19, 1938.

Lingulella acutangula BRIDGE (part), in Sellards, Adkins, and Plummer, Univ. Texas Bull. 3232, pl. 2, fig. 8, 1932.

This is a medium-sized species which falls between such species as *L. alia*, *L. burnetensis* and *L. bridgei*, on the one hand, and the small species like *L. texana*, *L. longula*, and *L. hilli* on the other. There is naturally variation in size. A large ventral valve is about 13 mm long and 8 mm wide.

The specimens from locality 68 are doubtfully referred to the species. In fact, it is not certain that all the others belong to one species.

Upper Cambrian, Cap Mountain; South Fork Morgan Creek, 4 miles northwest of Highway 29; Lion Mountain sandstone?; (loc. 68) near top of Packsaddle Mountain, 12 miles southeast of Llano; Wilberns; (loc. 69) Packsaddle Mountain, and (loc. 69) Honey Creek, 8 miles southeast of Llano, all in Texas.

Holotype.—U.S.N.M. no. 95017; paratypes, nos. 27410, 27412, 51644.

Lingulella nina (Walcott)

Obolus tetonensis nina WALCOTT (part), U. S. Geol. Surv. Mon. 51, p. 418, pl. 11, figs. 1-1g, 1912.

This species characterizes Honey Creek limestone of Oklahoma. The Texas form, from the slightly older Lion Mountain sandstone, formerly referred to *L. nina*, is a larger brachiopod.

Upper Cambrian, Honey Creek; (loc. 9r) 15 miles northwest of Fort Sill, and other localities in Oklahoma.

Holotype and paratypes.—U.S.N.M. no. 51643.

***Lingulella turneri*, n. sp.**

Lingulella (Lingulepis) acuminata WALCOTT (part), U. S. Geol. Surv. Mon. 51, p. 545, pl. 34, figs. 3a-d, 1912.

This form was apparently placed in *Lingulepis acuminata* because *L. nevadensis* was included with it.

L. turneri is characterized by an average size for the ventral valve, about 9 mm long and 6 mm wide. There is a tendency toward flattening of the front marginal outline.

Upper Cambrian, Emigrant; (locs. 7x, 7z) 2½ miles southeast of Benders Pass, Silver Peak Range, Nevada.

Cotypes.—U.S.N.M. nos. 56967, 51884.

LINGULEPIS Hall, 1863

***Lingulepis burnetensis*, n. sp.**

Lingulella (Lingulepis) acuminata WALCOTT (part), U. S. Geol. Surv. Mon. 51, p. 545, pl. 42, figs. 1k-n, 1912.

This species is smaller than either *Lingulella bridgei* or *Lingulepis llanoensis*. Compared with the latter *L. burnetensis* has about the same width, but the shell is shorter and the ventral valve tapers less evenly. One specimen 9 mm long is 6 mm wide.

Upper Cambrian, Wilberns; (loc. 70) Baldy Mountain, Morgans Creek, 8 miles northwest of Burnet, Texas.

Cotypes.—U.S.N.M. no. 51891.

***Lingulepis llanoensis*, n. sp.**

Lingulella (Lingulepis) acuminata WALCOTT (part), U. S. Geol. Surv. Mon. 51, p. 545, pl. 42, fig. 1, o, 1912.

Walcott figured only the interior of the dorsal valve, but a very fine example of the ventral valve lies against it. This species is slender, a ventral valve 12 mm long being only about 6 mm wide. The ventral valve tapers at a nearly even rate to the apex.

Upper Cambrian, Wilberns; (loc. 14b) Cold Creek, 2 miles south of the San Saba county line, Llano County, Texas.

Holotype and paratypes.—U.S.N.M. no. 51892.

Lingulepis nevadensis, n. sp.

Lingulella (Lingulepis) acuminata WALCOTT (part), U. S. Geol. Surv. Mon. 51, p. 545, pl. 34, figs. 3, 3e, 1912.

This brachiopod is associated with *Lingulella turneri* and evidently formed the basis on which Walcott referred both species to *L. acuminata*.

L. nevadensis is characterized by its relatively small size. Both figures of Walcott represent ventral valves, which show the usual degree of variation. The shell is not restricted toward the apex to any great extent. The growth lines are wavy.

Upper Cambrian, Emigrant; (loc. 7z) about 2½ miles southeast of Benders Pass, Silver Peak Range, Nevada.

Cotypes.—U.S.N.M. no. 51884.

ACROTRETIDAE Schuchert

ACROTHELE Linnarsson, 1876**Acrothele walcotti, n. sp.**

Acrothele colleni WALCOTT (part), U. S. Geol. Surv. Mon. 51, p. 640, text fig. 55, 1912; Smithsonian Misc. Coll., vol. 67, no. 2, p. 25, pl. 4, figs. 5-5c, 1917.

This species is characterized by the coarseness of both the ribs and the growth lines. The outline of both valves is more transverse than in *A. colleni*, from which *A. walcotti* further differs in the coarseness of the surface markings.

Middle Cambrian, Ross Lake shale; (loc. 35c) 1 mile east of Hector, Mount Bosworth; and (loc. 63j) Popes Peak, 1½ miles southwest of Stephen, British Columbia.

Holotype and paratypes.—U.S.N.M. no. 51410.

ACROTRETA Kutorga, 1848**Acrotreta aurumensis, n. sp.**

Acrotreta microscopica WALCOTT (part), U. S. Geol. Surv. Mon. 51, p. 693, pl. 67, figs. 2-2d, 1912.

Walcott recognized the distinctness of the Nevada species from *A. microscopica* but argued that the different shape was due to pressure. Neither the Texas nor the Nevada specimens are compressed or distorted. *A. aurumensis* has a more elevated ventral valve and is larger than *A. microscopica*. There is not as much variation in shape as is shown in the illustrations. In fact figure 2a is erroneously drawn, for that shell has the same outline as fig. 2.

This species is characterized by the erectness of the ventral valve so that the false area is about at right angles to the base of the shell.

Upper Cambrian; (loc. 8 o) 2 miles north of Aurum, Schell Creek Range, Nevada.

Cotypes.—U.S.N.M. no. 52119.

BILLINGSELLIDAE Schuchert

WIMANELLA Walcott, 1908

***Wimanella walcotti*, n. sp.**

Wimanella simplex WALCOTT (part), U. S. Geol. Surv. Mon. 51, p. 101, text fig. 64, 1912; Smithsonian Misc. Coll., vol. 67, no. 2, p. 26, pl. 4, figs. 7-7c, 1917.

This species is represented by many specimens in fine-grained, hard shale. Most of the ribbing and growth lines have been smoothed out by pressure. Fine ribs show in cross light and the growth lines must have been rather stronger than usual. The hinge line is straight and the undistorted valve forms a little more than a semicircle.

Middle Cambrian, Ross Lake; (loc. 63j) Popes Peak, 1½ miles south of Stephen; and 1 mile east of Hector, Mount Bosworth, British Columbia.

Cotypes.—U.S.N.M. nos. 63713-5, 51407.

***Wimanella rossensis*, n. sp.**

Wimanella simplex WALCOTT (part), Smithsonian Misc. Coll., vol. 67, no. 2, p. 26, pl. 4, figs. 8-8c, 1917.

Limestone nodules in the Ross Lake shale contain an abundant fauna among which is a species of *Wimanella* different from *W. walcotti* in the enclosing shale. Preservation in granular limestone in contrast to partial flattening in shale, accounts for some of the differences at first apparent. However, not all can thus be accounted for. *W. rossensis* is much higher in the ventral valve, thus creating a larger area. Growth lines are heavy, but vary more in size than in *W. walcotti*.

Middle Cambrian, Ross Lake; (loc. 63j) Popes Peak, 1½ miles south of Stephen; and 1 mile east of Hector, Mount Bosworth, British Columbia.

Cotypes.—U.S.N.M. nos. 64716-9.

GASTROPODA

PALAEACMAEIDAE Grabau and Shimer

HELCIONELLA Grabau and Shimer, 1909

Helcionella GRABAU and SHIMER, N. A. Index Foss., vol. 1, p. 607, 1909;
SMETANA, Roz Ceske Akad., vol. 27, no. 8, p. 3, 1918.

Grabau and Shimer erected *Helcionella* on *Stenotheca rugosa* without recognizing the fact that four species were included in Walcott's figures copied by them. Many of the numerous errors of generic reference and specific determination are not included in the present brief study. Confusion possibly still exists between *Helcionella* and *Stenotheca*. In fact, this and related, or similar forms, should undergo detailed monographic study in the near future.

Authors compare *Helcionella* with *Palaeacmacea*, distinguishing the former on the basis of the submarginal position and incurved shape of the apex. It may be that when the interior structure of *Helcionella* is obtained, the genus will be found to be synonymous with *Parmorphorella*, which it resembles outwardly.

Genotype: Mictoptoma? rugosa Hall.

Published species of *Helcionella* are listed together with their synonyms. New names and new species are then discussed.

Atlantic Province

Helcionella annulata Smetana

" (*Calloconus*) *ava* Smetana = *H. ava*

" *azus excentrica* Smetana = *H. excentrica*

" *cingulata* Cobbold

" *comleyensis* Cobbold

" ? *emarginata* Cobbold = *H. emarginata*

" *lata* Smetana

“ *lata glabra* Cobbold

" *maxima* Cobbold

" *media* Cobbold

" *oblonga* Cobbold

" *tombeckii* Cobbold

" cf. *rugosa* Kiaer = *H. kiacri*

" *rugosa acuticosta* Kiaer = *H. norvegica*

" *tjerozicensis* Smetana

" *tenuis* Smetana

North America

Helcionella cingulata ? Poulsen = Indeterminable fragment

" *elongata* Walcott { = *Stenothecoides elongata*
= " *labradorica*

“ *pricei* Resser and Howell

China

- Helcionella* ? *clivius* (Walcott) (Poorly preserved)
 “ *rugosa chinensis* (Walcott) = *H. chinensis*
Helcionella rugosa orientalis (Walcott) = { *H. orientalis*
 “ ? *simplex* Walcott
 “ *acuticosta pacifica* Saito = *H. pacifica*

***Helcionella rugosa* (Hall)**

- Meioptoma* ? *rugosa* HALL, Pal. New York, vol. 1, p. 306, pl. 83, fig. 6, 1847.
Stenotheca rugosa WALCOTT (part), U. S. Geol. Surv. Bull. 30, p. 128, pl. 12, figs. 1b, c, 1886 [not fig. 1 = *H. curticei*; 1a = *H. fordi*; 1d, e = *Stenothecoides troyensis*]; idem, 10th Ann. Rep., p. 617, pl. 74, figs. 1b, c, 1891 [not fig. 1 = *H. curticei*; 1a = *H. fordi*; 1d = *H. sp.*; 1e = *H. walcotti*; 1f, g = *H. halli*; 1h, i = *Stenothecoides troyensis*].
Helcionella rugosa Grabau and Shiner (part), N. A. Index Foss., vol. 1, p. 607, fig. 810b, 1909.

Great confusion was introduced into this species by illustration of the New York forms in 1886 and 1891. After that other workers assumed these animals to be highly variable and referred many diverse forms to *H. rugosa*.

Available specimens were segregated according to kind and locality. Thereupon, several species appeared as clearly defined units and are here defined. *H. rugosa* occurs only in the Hudson valley; at all other localities throughout the world the name was misapplied.

After careful comparison the name *rugosa* was restricted to the form which agrees with Hall's original description and illustration. Possibly if the original type could be studied this choice might have to be altered.

Lower Cambrian, Schodack; (loc. 27) Troy, and other localities, New York.

Holotype.—A.M.N.H. no. 212; plesiotypes, U.S.N.M. no. 15365.

***Helcionella halli*, n. sp.**

- Stenotheca rugosa* WALCOTT (part), 10th Ann. Rep. U. S. Geol. Surv., p. 617, pl. 74, fig. 1g, 1891 [see *H. rugosa*].

This species has a more circular outline than any other from New York. It is also high and has its apex overturned parallel to the base of the shell.

Lower Cambrian, Schodack; (loc. 35) 1½ miles north of Bald Mountain, northwest of Greenwich, New York.

Holotype.—U.S.N.M. no. 96472.

Helcionella walcotti, n. sp.

Stenotheca rugosa WALCOTT (part), 10th Ann. Rep. U. S. Geol. Surv., p. 617, pl. 74, fig. 1c, 1891 [see *H. rugosa*].

This is the most common species in the Hudson valley. It has the coarsest ribs, and differs further in that the ribs are angular while in other species they are rounded in contour.

Lower Cambrian, Schodack; (loc. 33) North Greenwich, and many other localities in New York.

Holotype.—U.S.N.M. no. 17456.

Helcionella curticei, n. sp.

Stenotheca rugosa WALCOTT (part), U. S. Geol. Surv. Bull. 30, p. 128, pl. 12, fig. 1, 1886; idem, 10th Ann. Rep., p. 617, pl. 74, fig. 1, 1891 [see *H. rugosa*].

The holotype lies in the matrix, besides a good example of *H. rugosa*, so that it is easy to compare the two. *H. curticei*, which is named for the collector, is twice as high as *H. rugosa*, has a more rounded elliptical outline and coarser ribbing.

Lower Cambrian, Schodack; (loc. 27) Troy, New York.

Holotype.—U.S.N.M. no. 96473.

Helcionella fordii, n. sp.

Stenotheca rugosa WALCOTT (part), U. S. Geol. Surv. Bull. 30, p. 128, pl. 12, fig. 1a, 1886; idem, 10th Ann. Rep., p. 617, pl. 74, fig. 1a, 1891 [see *H. rugosa*].

H. fordii has a much rounder elliptical outline than *H. rugosa*. The rugosity is stronger than in *H. curticei*, from which *H. fordii* further differs in greater relative height.

Occurrence same as preceding.

Holotype.—U.S.N.M. no. 96474.

Helcionella tatei, n. sp.

Stenotheca rugosa Tate, Trans. Roy. Soc. South Australia, vol. 15, p. 183, pl. 2, fig. 4, 1892.

This species is characterized by its wide base. The sides slope evenly and the apex is overturned, but only near its tip. As shown in the figure the ribs are angular, but they are not pronounced. There are also vertical striations.

Lower Cambrian; Androssan, South Australia.

Holotype.—Australia; plastotypes, U.S.N.M. no. 96475.

Helcionella sp.

Stenotheca rugosa WALCOTT (part), 10th Ann. Rep. U. S. Geol. Surv., p. 617, pl. 74, fig. 1d, 1891 (see *H. rugosa*).

This Atlantic Province form referred to *H. rugosa* cannot be found in the collections as it evidently never was properly marked as a type. Until the specimen is located, its description cannot be written.

Lower Cambrian, Etcheminian; Conception Bay, Newfoundland.

Helcionella kiaeri, n. sp.

Helcionella cf. *rugosa* KIAER, Skft. Vid. Kristiania, 1916, Mat.-Natur. Kl., vol. 2, p. 19, pl. 2, fig. 3, 1917.

This is a rather stout, coarse-ribbed form but is not as large as some of the New York species. Its outline is evidently nearly circular.

Lower Cambrian, *Strenuella* limestone; Tømten, Ringsaker, Norway.

Holotype.—Pal. Mus. Oslo. no. 61b.

Helcionella norvegica, n. sp.

Helcionella rugosa acuticosta KIAER, Skft. Vid. Kristiania, 1916, Mat.-Natur. Kl., vol. 2, p. 20, pl. 2, figs. 4, 4a, 1917.

This is a small form characterized by strongly curved outlines front and back, with the apex turned beyond 90°. The ribs are sharply angled.

Occurrence same as preceding.

Holotype.—Pal. Mus. Oslo no. 15.

Helcionella erecta (Walcott)

Stenotheca rugosa erecta WALCOTT, 10th Ann. Rep. U. S. Geol. Surv., p. 617, pl. 74, fig. 4, 1891.

Lower Cambrian, Etcheminian; (loc. 41) Manuels Brook, Conception Bay, Newfoundland.

Holotype.—U.S.N.M. no. 18311.

Helcionella acutacosta (Walcott)

Stenotheca ? rugosa acutacosta WALCOTT, 10th Ann. Rep. U. S. Geol. Surv., p. 617, pl. 74, figs. 2-2b, 1891.

Occurrence same as preceding.

Lectotype (fig. 2) and *paratype*.—U.S.N.M. no. 18310.

Helcionella curvirostra (Shaler and Foerste)

Stenotheca curvirostra SHALER and FOERSTE, Mus. Comp. Zool., Bull. 16, p. 30, pl. 1, fig. 8, 1888; WALCOTT, 10th Ann. Rep. U. S. Geol. Surv., p. 618, pl. 74, fig. 10, 1891.

Lower Cambrian, Hoppin; North Attleboro, Massachusetts.

Holotype.—U.S.N.M. no. 96476.

***Helcionella cobboldi*, n. sp.**

Stenotheca abrupta ? COBBOLD, Geol. Mag., dec. 6, vol. 4, p. 156, pl. 4, figs. 28, 29, 1919.

This species is similar to *H. abrupta*, but differs in being more slender and the ribs do not project so far beyond the marginal outline of the shell.

Lower Cambrian, Hartshill; Nuneaton, Warwickshire, England.

Cotypes.—Sedgwick Mus.

***Helcionella abrupta* (Shaler and Foerste)**

Stenotheca abrupta SHALER and FOERSTE, Bull. Mus. Comp. Zoöl., vol. 16, p. 29, pl. 1, figs. 9a, b, 1888; WALCOTT, 10th Ann. Rep. U. S. Geol. Surv., p. 617, pl. 74, figs. 6, 6a, 1891.

Only the smaller of Foerste's specimens is to be found in the collections. These types were never marked and the material is rather fragile. The species must be restricted to the form first described.

Lower Cambrian, Hoppin; North Attleboro, Massachusetts.

Cotypes.—U.S.N.M. no. 96477.

***Helcionella alia*, n. sp.**

Stenotheca curvirostra GRABAU, Occ. Papers Boston Soc. Nat. Hist., vol. 4, p. 638, pl. 31, fig. 13, 1900; GRABAU and SHIMER (not Shaler and Foerste), N. A. Index Foss., vol. 2, p. 373, fig. 1674d, 1910.

This species is stouter and longer than *H. curvirostra* and has more numerous ribs.

Lower Cambrian, Weymouth; Sandy Cove, Cohasset, Massachusetts.

Holotype.—Boston Soc. Nat. Hist. no. 11964.

***Helcionella grabau*, n. sp.**

Stenotheca abrupta GRABAU (not Shaler and Foerste), Occ. Papers Boston Soc. Nat. Hist., vol. 4, p. 637, pl. 31, figs. 12a-c, 1900; GRABAU and SHIMER, N. A. Index Foss., vol. 2, p. 373, figs. 1674a-c, 1910.

This is an erect species, but even then is more curved than *H. abrupta*. Grabau's original figures do not agree one with the other, but angle of view and the difference between mold of interior and exterior would account for this. This species is characterized by the large number of annulations, 10 being shown in the figure.

Lower Cambrian, Weymouth; Nahant, Massachusetts.

Cotypes.—Boston Soc. Nat. Hist. no. 11962.

Helcionella pauper (Billings)

Stenotheca pauper BILLINGS, Canadian Nat., new ser., vol. 6, p. 479, 1872.

Stenotheca rugosa paupera WALCOTT, 10th Ann. Rep. U. S. Geol. Surv., p. 617, pl. 74, fig. 7, 1891.

This species must be restricted to the form from Newfoundland. Billings's type was not figured, but Walcott states that he compared the type with the specimen he figured in 1891.

Lower Cambrian, Etcheminian; (loc. 41) Manuels Brook, Conception Bay, Newfoundland.

Holotype.—Nat. Mus. Canada; plesiotype, U.S.N.M. no. 18312.

Helcionella foerstei, n. sp.

Stenotheca rugosa pauper SHALER and FOERSTE, Bull. Mus. Comp. Zoöl., vol. 16, p. 29, pl. 1, fig. 7, 1888.

Compared with the specimen Walcott figured as *H. pauper*, the Massachusetts species is much more curved and has stronger ribs.

Lower Cambrian, Hoppin; North Attleboro, Massachusetts.

Holotype.—U.S.N.M. no. 96478.

Helcionella terranovica, n. sp.

Stenotheca ? rugosa levis WALCOTT (part), 10th Ann. Rep. U. S. Geol. Surv., p. 617, pl. 74, fig. 5, 1891 (see *H. levis*).

This is a much taller and stouter form than the other specimen Walcott referred to his variety *levis*. This species is stouter and more erect than *H. levis* and has fewer, much larger, annulations.

Lower Cambrian, Etcheminian; (loc. 41) Manuels, Conception Bay, Newfoundland.

Holotype.—U.S.N.M. no. 96479.

Helcionella striata, n. sp.

Stenotheca levis GRABAU (not Walcott), Occ. Paper Boston Soc. Nat. Hist., vol. 4, p. 641, pl. 31, fig. 15, 1900.

This form is shaped somewhat like *H. terranovica*, but the illustration shows pronounced longitudinal striations.

Lower Cambrian, Weymouth; Pleasant Beach, Cohasset, Massachusetts.

Holotype.—Boston Soc. Nat. Hist. no. 11961.

Helcionella recurva, n. sp.

Stenotheca pauper GRABAU (not Billings), Occ. Papers Boston Soc. Nat. Hist., vol. 4, p. 639, pl. 31, fig. 14, 1900; Grabau and Shimer, N. A. Index Foss., vol. 2, p. 374, fig. 1674c, 1910.

This species is much more curved than *H. foerstei* and besides has coarser ribs.

Lower Cambrian, Weymouth; Sandy Cove, Cohasset, Massachusetts.

Holotype.—Boston Soc. Nat. Hist. no. 11963.

***Helcionella levis* (Walcott)**

Stenotheca ? rugosa levis WALCOTT (part), 10th Ann. Rep. U. S. Geol. Surv., p. 617, pl. 74, fig. 5a, 1891.

Walcott included two forms in his variety *levis*. The smoother one is chosen to represent the species and the other described as *H. terranovaica*.

Lower Cambrian, Etcheminian; (loc. 41) Manuels, Conception Bay, Newfoundland.

Holotype.—U.S.N.M. no. 18313.

***Helcionella elevata* (Cobbold)**

Scenella elevata COBBOLD, Quart. Journ. Geol. Soc. London, vol. 76, pt. 4, p. 364, pl. 24, fig. 36, 1921.

Cobbold pointed out that this species did not conform to the requirements of *Scenella* but because it lacked pronounced concentric rugosities reference to *Helcionella* was more difficult. Now that wide variation in this respect is known to exist in *Helcionella*, the shape of *H. elevata* may be relied on and the species referred to *Helcionella*.

Lower Cambrian, *Olenellus* limestone; Comley, Shropshire, England.

Holotype.—Geol. Surv. no. RR1211.

***Helcionella wheeleri* (Walcott)**

Stenotheca wheeleri WALCOTT, Canadian Alpine Journ., vol. 1, no. 2, pl. 1, fig. 7, 1908.

Middle Cambrian, Stephen; (loc. 14s) Mount Stephen, near Field, British Columbia.

Holotype.—U.S.N.M. no. 96480.

***Helcionella belliana* (Walcott)**

Platyccras (?) belliana WALCOTT, Canadian Alpine Journ., vol. 1, no. 2, pl. 1, fig. 13, 1908.

Occurrence same as preceding.

Holotype.—U.S.N.M. no. 96481.

***Helcionella romingeri* (Walcott)**

Platyccras romingeri WALCOTT, Proc. U. S. Nat. Mus., vol. 11, p. 442, 1888; Canadian Alpine Journ., vol. 1, no. 2, pl. 1, fig. 14, 1908.

Middle Cambrian, Stephen: (loc. 14s) Mount Stephen, near Field, British Columbia.

Holotype.—U.S.N.M. no. 96482.

***Helcionella orientalis* (Walcott)**

Stenotheca rugosa orientalis WALCOTT, Proc. U. S. Nat. Mus., vol. 29, p. 16, 1905.

Helcionella rugosa orientalis WALCOTT (part), Research in China, vol. 3, Carnegie Inst. Publ. 54, p. 91, pl. 5, fig. 15a, 1913 (not fig. 15 = *H. shantungensis*).

The species is restricted to the form at the first locality, which according to Dr. Walcott's practice is the type locality.

Middle Cambrian, Changhia; (loc. C21) Changhia, Shantung, China.

Holotype.—U.S.N.M. no. 57776.

***Helcionella shantungensis*, n. sp.**

Helcionella rugosa orientalis WALCOTT (part), Research in China, vol. 3, Carnegie Inst. Publ. 54, p. 91, pl. 5, fig. 15, 1913 (see *H. orientalis*).

This species is wider at the base than *H. orientalis* and the rugosities are not so coarse. The striations are also finer and weaker.

Middle Cambrian, Changhia; (loc. C18) east of Changhia, Shantung, China.

Holotype.—U.S.N.M. no. 57775.

***Helcionella triangularis* (Matthew)**

Stenotheca triangularis MATTHEW, Trans. Roy. Soc. Canada, vol. 3, sec. 4, p. 58, pl. 6, figs. 15, 15a, 1886.

Middle Cambrian, St. John; Hanford Brook, New Brunswick.

Holotype and paratype.—Walker Mus. (?).

***Helcionella manuelensis* (Matthew)**

Plumulites manuelensis MATTHEW, Trans. New York Acad. Sci., vol. 15, p. 145, fig. 1, 1896.

Middle Cambrian, Manuels; Manuels Brook, Conception Bay, Newfoundland.

Holotype.—Walker Mus. (?).

SCENELLA Billings, 1872

Diverse forms are referred to *Scenella*, particularly post-Cambrian species. A list of Cambrian species referred to the genus is given with cross references.

Atlantic Province

- Scenella antiqua* Kiaer
 " *depressa* Kiaer
 " ? *discinoides* Schmidt (possibly two species)
 " *elevata* Cobbold = *Helcionella elevata*
 " *reticulata* Billings
 " ? *tuberculata* Schmidt

North America

- Scenella conula* Walcott
 " *retusa* Ford = (part = *Paterina troyensis*)
 " *varians* Walcott = (part *S. amii*)
 " *amii* Matthew

China

- Scenella clotho* Walcott = *Scenellopsis clotho*
 " " Saito = *S. saitoi*
 " *dilatatus* Walcott = *S. dilatata*

Scenella amii (Matthew)

Metoptoma amii MATTHEW, Trans. Roy. Soc. Canada, 2nd ser., vol. 8, sec. 4, p. 111, pl. 1, fig. 12, 1902.

Scenella varians WALCOTT, Canadian Alpine Journ., vol. 1, no. 2, pl. 1, fig. 6, 1908.

[Not *Scenella varians* WALCOTT, U. S. Geol. Surv. Bull. 30, p. 127, pl. 12, figs. 2, 2a, 1886.]

Middle Cambrian, Stephen: (loc. 14s) Mount Stephen, near Field, British Columbia.

Holotype.—Walker Mus. (?); plesiotype, U.S.N.M. no. 96483.

Scenella columbiana (Walcott)

Crania ? columbiana WALCOTT, Proc. U. S. Nat. Mus., vol. 11, p. 441, 1889.

Philhedra ? columbiana VON HUENE, Verhandl. Russ.-kais. Min. Gesell. St. Petersburg, 2nd ser., vol. 36, pt. 2, pp. 216, 298, 1899.

Philhedra columbiana WALCOTT, U. S. Geol. Surv. Mon. 51, p. 724, pl. 81, fig. 10, 1912.

Walcott reports the finding of two additional imperfect specimens in 1907. Examination of these specimens leads one to doubt their identity with the type. It is possible that they are merely the apical portions of *Nisusia*.

The type is a minute form not very well preserved. It certainly is not a brachiopod, so the best reference is to *Scenella*. This specimen may be merely a poorly or rather unusually preserved example of *Scenella amii*. However, since no other such example has been noted among the hundreds of *Scenella amii* specimens in the collection, this form may retain its specific rank.

Middle Cambrian; (loc. 14s) Mount Stephen, above Field, British Columbia.

Holotype.—U.S.N.M. no. 58307.

SCENELLOPSIS, n. gen.

A peculiar form from China, referred with reservation to *Scenella*, seems to be a gastropod.

Scenellopsis is a small limpetlike shell with somewhat eccentric apex. Both growth and radiating lines are present but are preserved in two different specimens. Muscular impression, evidently branching, produces folds on the outer surface.

Genotype.—*Scenella clotho* Walcott.

***Scenellopsis dilatata* (Walcott)**

Scenella ? dilatatus WALCOTT, Proc. U. S. Nat. Mus., vol. 30, p. 570, 1906; Research in China, vol. 3, Carnegie Inst. Publ. 54, p. 87, pl. 5, figs. 2, 2a, 1913.

Middle Cambrian, Changhia; (loc. C70) southeast of Tungyü, Shansi, China.

Cotypes.—U.S.N.M. nos. 57767, 8.

***Scenellopsis clotho* (Walcott)**

Scenella clotho WALCOTT, Proc. U. S. Nat. Mus., vol. 29, p. 12, 1905; Research in China, vol. 3, Carnegie Inst. Publ. 54, p. 86, pl. 5, figs. 3, 3a, 1913.

Middle Cambrian, Changhia; (loc. C18) East of Changhia, Shantung, China.

Holotype.—U.S.N.M. no. 57769.

***Scenellopsis saitoi*, n. sp.**

Scenella clotho SAITO (not Walcott), Journ. Faculty Sci. Imp. Univ. Tokyo, sec. 2, vol. 4, pt. 3, p. 359, pl. 3, figs. 18, 19, 1936.

This species resembles *S. clotho*, but, as pointed out by Saito, the apex is not as high and the apertural margin is less upturned. Saito's figures show that the marginal outline is also much more flattened at the broad end.

Lower Cambrian, Misaki; near Chungwa, northern Chosen.

Holotype.—Geol. Inst. Imp. Univ. Tokyo.

HYOLITHES Eichwald, 1840

Eichwald established *Hyolithes* on *H. acutus* from Ordovician strata of Estonia. The genus seems to be valid for other species extending from the Lower Cambrian into the Devonian. In the earlier years *Hyolithes* was confused with various cephalopod genera, particularly *Orthoceras* but this confusion was cleared up long ago. Several authors attempted classification of the family but no one has completed the job.

Matthew erected the genus *Camarotheca* for the hyolithid forms which show internal septa and a structure analogous to the cephalopod siphuncle. Examination of many species shows that cameration depends on preservation and may be found in any species. The other genera excepting *Camarotheca* are apparently all valid, or at any rate express definite and distinctive structures.

Orthotheca Novak is valid only for Ordovician organisms, which are unrelated to the rounded tubes oftentimes placed in *Hyolithes*. Therefore, the practice, followed by the author and others, of assigning tapered tubes with circular cross-section to *Orthotheca*, is improper.

Revision of Cambrian Hyolithidae is greatly needed. Not only must a series of genera be established but the species themselves have been so carelessly handled that most are of little value. Recent stratigraphic studies occasioned review, in part, of *H. primordialis* and *H. billingsi*. Several of the resulting nomenclatural changes are recorded below.

***Hyolithes gregarius* (Meek and Hayden)**

Theca (Pugiunculus) gregaria MEEK and HAYDEN, and Proc. Acad. Nat. Sci. Philadelphia, p. 436, 1861; Amer. Journ. Sci., 2d ser., vol. 33, p. 73, text fig. 3, 1862.

Theca gregaria MEEK and HAYDEN, Pal. Upper Missouri, Smithsonian Contr. Knowl., vol. 7, p. 5, text figs. a-d, 1865.

This species averages much smaller than *H. primordialis* to which it was referred and, therefore, is again recognized.

Upper Cambrian, Depass; Powder River, Big Horn Mountains, Wyoming.

Cotypes.—U.S.N.M. no. 1181.

***Hyolithes gallatinensis*, n. sp.**

Hyolithes primordialis WALCOTT (part), U. S. Geol. Surv. Mon. 32, pt. 2, p. 454, pl. 63, fig. 2, 1899.

This wide species is characterized by a very slightly convex posterior surface and an evenly, semicircular anterior side. The surface is smooth in the specimens available but they may be interiors only. The lingual extension is broken away.

Upper Cambrian, Dry Creek; (loc. 151c) Crowfoot Ridge, Gallatin Range, Yellowstone National Park, Wyoming.

Holotype.—U.S.N.M. no. 35218.

***Hyolithes whitei*, n. sp.**

Hyolithes primordialis ? WHITE, Geogr. Geol. Expl. Surv. West 100th Merid., Prelim. Rep. Invert. Foss., p. 6, 1874. Idem, vol. 4, pt. 1, p. 37, pl. 1, figs. 5a-e, 1875.

Hyolithes billingsi WALCOTT (part), U. S. Geol. Surv. Bull. 30, p. 134, pl. 13, figs. 1, 1a-d, 1886; idem, 10th Ann. Rep., p. 620, pl. 75, figs. 1, 1a-d, 1891; LESLEY (part), Geol. Surv. Pennsylvania, Rep. P4, p. 294, figs. 1889; GRABAU and SHIMER, N. A. Index Foss., vol. 2, p. 3, figs. 1211e-g, 1910.

H. whitei is a rather small species with a thick shell. The posterior side is nearly flat; the anterior is angulated giving the tube a nearly equilateral triangular outline. The lateral corners are rounded.

Lower Cambrian, Pioche; (loc. 31a) southeast of Pioche, Highland Range, Nevada.

Cotypes.—U.S.N.M. nos. 8579, 15377.

***Hyolithes poulsenii*, n. sp.**

Hyolithes billingsi POULSEN, Meddels. Grønland, vol. 70, p. 254, pl. 15, figs. 26, 27, 1927.

Hyolithus (*Hyolithus*) *billingsi* POULSEN, idem, vol. 87, no. 6, p. 22, pl. 3, fig. 6, 1932.

This species has a flat posterior side and a rounded anterior face. It expands much more rapidly and is larger than *H. billingsi*. The anterior surface is striated.

Lower Cambrian, Cape Kent; Cape Kent, North Greenland. Bastion; Hyolithus Creek, East Greenland.

Cotypes and plesiotypes.—Min. Mus. Copenhagen; plastotypes, U.S.N.M. no. 70951.

CRUSTACEA

STENOTHECA Salter, 1872

Stenotheca HICKS (Salter MSS.), Quart. Journ. Geol. Soc. London, vol. 28, p. 180, 1872; WALCOTT, U. S. Geol. Surv. Bull. 30, p. 128, 1886; MATTHEW, Trans. Roy. Soc. Canada, vol. 8, p. 132, 1891; GRABAU and SHIMER, N. A. Index Foss., vol. 2, p. 373, 1910; COBBOLD, Geol. Mag., vol. 71, p. 463, 1934.

Watsonella GRABAU, Occ. Pap. Boston Soc. Nat. Hist., vol. 4, p. 631, 1900.

Stenotheca, a generic name attached to museum specimens, was published without description in 1872. In 1886 Walcott described the genus but quite clearly based his remarks on *Helcionella rugosa* and its allies. Consequently his description is that of the gastropod genus *Helcionella*. More recently Cobbold restudied Salter's types and presented a generic diagnosis.

In 1891 Matthew recognized the crustacean characters of *Stenotheca*, in which he was followed by Grabau and Shimer. The latter, however, assigned only gastropod species to the genus. Cobbold assigns the genus to the Notostraca.

It will be observed that Cobbold's generic description of *Stenotheca* agrees in every detail with that of *Watsonella* Grabau. The illustrations also agree; therefore *Watsonella* must be regarded as a synonym of *Stenotheca*.

All known species of *Stenotheca* are confined to the Atlantic province.

Genotype.—*S. cornucopia* Salter.

The following are regarded as valid species of *Stenotheca*:

<i>S. angusta</i> Cobbold	<i>S. hicksiana</i> Matthew
<i>S. concentrica</i> Matthew	<i>S. lata</i> Cobbold
<i>S. cornu</i> Wiman	<i>S. nasuta</i> Matthew
<i>S. cornucopia</i> Salter	<i>S. radiata</i> Matthew
<i>S. crosbyi</i> (Grabau)	

Species formerly referred to *Stenotheca* are given, together with their synonyms.

<i>S. abrupta</i> ? Cobbold	= <i>Helcionella cobboldi</i>
<i>S. abrupta</i> Grabau and Shimer	= <i>H. grabaui</i>
<i>S. abrupta</i> Shaler and Foerste	= <i>H. abrupta</i>
<i>S. (Parmorphorella) acadica</i> Matthew	= <i>Parmorphorella acadica</i>
<i>S. clurius</i> Walcott	= <i>Helcionella ? clurius</i>
<i>S. curvirostra</i> Grabau	= <i>H. alia</i>
<i>S. curvirostra</i> Shaler and Foerste	= <i>H. curvirostra</i>
<i>S. elongata</i> Walcott	= { <i>Stenothecoides elongata</i> <i>S. labradorica</i>
<i>S. levis</i> Grabau	= <i>Helcionella striata</i>
<i>S. pauper</i> Billings	= <i>H. pauper</i>
<i>S. pauper</i> Grabau	= <i>H. recurva</i>
<i>S. rugosa</i> Billings	= <i>H. rugosa</i>
<i>S. rugosa</i> Walcott	= { <i>H. curticei</i> <i>H. fordi</i> <i>H. walcotti</i> <i>H. halli</i> <i>Stenothecoides troyensis</i>
<i>S. rugosa</i> Sears	= <i>Helcionella abrupta</i>
<i>S. rugosa</i> Tate	= <i>H. tatei</i>
<i>S. ? rugosa acutacosta</i> Walcott	= <i>H. acutacosta</i>
<i>S. rugosa aspera</i> Noetling	= <i>Pseudotheca waageni</i>
<i>S. rugosa erecta</i> Walcott	= <i>Helcionella erecta</i>
<i>S. rugosa chinensis</i> Walcott	= <i>H. chinensis</i>
<i>S. ? rugosa levis</i> Walcott	= <i>H. levis</i>
<i>S. rugosa orientalis</i> Walcott	= <i>H. orientalis</i>
<i>S. rugosa pauper</i> Shaler and Foerste	= <i>H. foerstei</i>
<i>S. rugosa paupera</i> Walcott	= <i>H. pauper</i>
<i>S. simplex</i> Walcott	= <i>H. ? simplex</i>
<i>S. triangularis</i> Matthew	= <i>H. triangularis</i>
<i>S. wheeleri</i> Walcott	= <i>H. wheeleri</i>

***Stenotheca crosbyi* (Grabau)**

Watsonella crosbyi GRABAU, Occ. Pap. Boston Soc. Nat. Hist., vol. 4, p. 632, pl. 31, figs. 9a-f, 1900.

Lower Cambrian, Weymouth; Pleasant Beach and Sandy Cove, Cohasset, Massachusetts.

Cotypes.—Boston Soc. Nat. Hist. nos. 11951-11954.

STENOTHECOIDES, n. gen.

Stenothecoides is related to *Stenotheca*, but is much narrower and longer, with, a relatively wider aperture. The genus is characterized by the long narrow carapace which is curved longitudinally. This curvature is usually much greater in cross-section, amounting to a fold along the apex. The apertural outline increases from the narrow anterior end almost evenly to a broadly rounded rear margin. The marginal outline of some species is not bilaterally symmetrical, curving out more on one side than the other. The surface is marked with growth lines surrounding the anterior end, each extending itself rearward at a greater rate, so that while the anterior ends remain close together, the lines become longer and longer, reaching to the posterior portion of the test.

Genotype.—*Stenotheca clongata* Walcott.

***Stenothecoides elongata* (Walcott)**

Stenotheca clongata WALCOTT, U. S. Geol. Surv. Mon. 8, p. 23, pl. 9, figs. 2, 2a, 1884; idem (part), Bull. 30, p. 129, pl. 12, figs. 4a, b, 1886 (not fig. 4 = *S. labradorica*).

Helcionella clongata WALCOTT, Smithsonian Misc. Coll., vol. 67, no. 3, p. 63, 1917.

Middle Cambrian, Eldorado; (loc. 55b) West slope Prospect Peak, Eureka District, Nevada.

Holotype.—U.S.N.M. no. 15364.

***Stenothecoides labradorica*, n. sp.**

Stenotheca clongata WALCOTT (part), U. S. Geol. Surv. Bull. 30, p. 129, pl. 12, fig. 4, 1886.

This species was identified with that from the Eureka District, Nevada, but the drawing shows that it is clearly distinct. *S. labradorica* is shorter and wider and the apertural margin evidently is not as symmetrical as *S. clongata*. The growth lines are also somewhat weaker.

Lower Cambrian, Forteau; L'Anse au Loup, Labrador.

Holotype.—U.S.N.M. no. 14883.

Stenothecoides troyensis, n. sp.

Stenotheca rugosa WALCOTT (part), U. S. Geol. Surv. Bull. 30, p. 128, pl. 12, figs. 1d, e, 1886 (see *Helcionella rugosa*); idem, 10th Ann. Rep., p. 617, pl. 74, figs. 1h, i, 1891.

This a very small species, and is much wider than any of the others. Longitudinal curvature is accentuated at the anterior end so that a slightly recurved apex is developed.

Lower Cambrian, Schodack; (loc. 27) Troy, and other localities in New York.

Holotype.—U.S.N.M. no. 96484.

Stenothecoides poulsenii, n. sp.

Undetermined lamellibranch POULSEN, Meddels Grønland., vol. 87, no. 6, p. 29, pl. 7, figs. 1-4, 1932.

It is possible that more than one species is represented by the specimens illustrated. Growth lines are coarse and irregular. This species is so constricted laterally toward the anterior end as to form a distinct apex.

Lower Cambrian, Ella Island; south coast Ella Island, east Greenland.

Cotypes.—Min. Mus. Copenhagen.

TUZOIA Walcott, 1912**Tuzoia argenta (Walcott)**

Leperditia? argenta WALCOTT, U. S. Geol. Surv. Bull. 30, p. 146, pl. 8, fig. 5, 1886.

Middle Cambrian, Ophir; (loc. 30a) 1 mile below Argenta, Big Cottonwood Canyon, Wasatch Mountains; and (loc. 54a) Blacksmith Fork, Bear River Range, Utah.

Holotype.—U.S.N.M. no. 15401.

UNCERTAIN POSITION**UROTHECA Matthew, 1899****Urotheca parasitum, n. sp.**

Hyolithellus flagellum WALCOTT (part), Smithsonian Misc. Coll., vol. 67, no. 2, p. 26, pl. 5, fig. 2a, 1917.

This species consists of narrow, long flexible tubes which had one or more longitudinal grooves. It is a much smaller tube than *U. flagellum*. The type and other specimens grew on shells of *Wimanelia*, which raises the question whether all species of *Urotheca* had such growth habit.

Middle Cambrian, Ptarmigan; (loc. 63j) Popes Peak, $1\frac{1}{2}$ miles southwest of Stephen, and (loc. 35c) Mount Bosworth, British Columbia.

Cotypes.—U.S.N.M. no. 63723.

COLEOLOIDES Walcott, 1890

Coleoloides hectori (Walcott)

Hyolithellus hectori WALCOTT, Smithsonian Misc. Coll., vol. 67, no. 2, p. 27, pl. 5, fig. 1, 1917.

This species is referred to *Colcoloides* on the basis of its shape and the presence of striations. It differs from *C. typicalis* in that the striations are coarser, and the tube itself is of greater diameter. Too little of the tube preserves the striated outer surface to show whether the striations in *C. hectori* have a spiral course, but they seem to be slightly off parallel position in the short portion preserved.

Middle Cambrian, Ross Lake; (loc. 35c) 1 mile east of Hector, Mount Bosworth, British Columbia.

Holotype.—U.S.N.M. no. 63721.

AGNOSTIDA

AGNOSTUS Brongniart, 1822

Agnostus yellowstonensis, n. sp.

Agnostus bidens WALCOTT, U. S. Geol. Surv. Mon. 32, pt. 2, p. 455, pl. 63, figs. 4, 4a, 1899.

This species is not the same as the Middle Cambrian *A. bidens* Meek. It is characterized by strong dorsal furrows in both shields, the anterior glabellar lobe being sharply separated. The published illustration of the pygidium is misleading because the artist failed to eliminate perspective when drawing the convex shield and therefore extended the axis too far rearward. In fact the space between the rhachis and rear margin is half the width of the pleural lobes.

Upper Cambrian, Dry Creek; (loc. 151c) Crowfoot Ridge, Gallatin Range, Yellowstone National Park, Wyoming.

Cotypes.—U.S.N.M. no. 35222.

TRILOBITA

BAILIELLA Matthew, 1885

Bailiella RESSER, Smithsonian Misc. Coll., vol. 95, no. 4, p. 15, 1936.

Several species must be added to the list published in 1936. Some of them were overlooked, one correction was expected to appear elsewhere and others have since been described under *Conocoryphe*.

Bailiella artagena (Howell)

Conocoryphe? artagena HOWELL, Bull. Geol. Soc. Amer., vol. 48, no. 8, p. 1169, pl. 3, fig. 7, 1937.

Middle Cambrian, St. Albans; St. Albans, Vermont.

Holotype.—Princeton Univ. no. 9925.

Bailiella frangtengensis (Reed)

Conocoryphe frangtengensis REED, Mem. Geol. Surv. India, Pal. Ind., new ser., vol. 21, mem. 2, p. 7, pl. 2, figs. 9-12, 1934.

Middle Cambrian; Frangteng Hill, Hundwara, Kashmir, India.

Cotypes.—Geol. Surv. India nos. 15593-6.

Bailiella lantenoisi (Mansuy)

Conocoryphe lantenoisi MANSUY, Mem. Serv. Geol. l'Indo-Chine, vol. 5, fasc. 1, p. 30, pl. 4, figs. 6, 7; pl. 5, fig. 3, 1916; KOBAYASHI, Journ. Faculty Sci. Imp. Univ. Tokyo, sec. 2, vol. 4, pt. 2, p. 218, pl. 23, figs. 13, 14, 1935.

Middle Cambrian; Tien-fong, Tonkin.

Bailiella sejuncta (Reed)

Conocoryphe sejuncta REED, Mem. Geol. Surv. India, Pal. Ind., new ser., vol. 21, mem. 2, p. 8, pl. 2, figs. 13, 14, 1934.

Middle Cambrian; Wadapur, Hundwara, Kashmir, India.

Cotype.—Geol. Surv. India nos. 15597-8.

Bailiella ulrichi (Resser and Endo)

Conocoryphe ulrichi RESSER and ENDO, in Endo, Iwanami Lecture Ser., Geol. Pal., p. 54, figs. 5-8, December 1931.

Middle Cambrian, Tangshih; Tang-shih-ling, 2 miles southeast Yen-tai Colliery, Manchoukuo.

BLOUNTIA Walcott, 1916**Blountia polita, n. sp.**

Arionellus sp. WALCOTT, U. S. Geol. Surv. Mon. 32, pt. 2, p. 463, pl. 65, fig. 2, 1899.

Walcott illustrated this pygidium as a cranidium. The artist drew "glabellar" furrows, but when his pencil marks were washed off the specimen, no trace of axial furrows remain.

B. polita is characterized by its flat lateral profile, and the rather elongate shape due to the lack of narrowing as the pleural lobes unite behind the axis. The dorsal furrow is shallow, but the axis is marked rather clearly by a change in the profile.

Upper Cambrian, Pilgrim; (loc. 151b) between Pebble and Soda Butte Creeks, Yellowstone National Park, Wyoming.

Holotype.—U.S.N.M. no. 96488.

BRISCOIA Walcott, 1924

Briscoia texana (Walcott)

Dikelocephalus texanus WALCOTT, Smithsonian Misc. Coll., vol. 57, no. 13, p. 372, pl. 65, fig. 4, 1914.

Upper Cambrian, Wilberns; (loc. 70a) Baldy Mountain, near Morgans Creek, 8 miles northwest of Burnet, Texas.

Holotype.—U.S.N.M. no. 58621.

CHARIOCEPHALUS Hall, 1863

Chariocephalus HALL, 16th Ann. Rep. New York State Cab. Nat. Hist., p. 175, 1863.

Dartonaspis MILLER, Journ. Pal., vol. 10, no. 1, p. 29, 1936.

Miller failed to observe that the criteria on which he based *Dartonaspis* are exactly those which led to the separation of *Irvingella* from *Chariocephalus*. These relationships are discussed under *Irvingella*.

Chariocephalus knighti (Miller)

Dartonaspis knighti MILLER, Journ. Pal., vol. 10, no. 1, p. 29, pl. 8, figs. 34, 35, 1936.

Upper Cambrian, Boysen; Bull Lake Creek, Wind River Range, Wyoming.

Holotype.—Columbia Univ. no. 12626.

CLEVELANDELLA Resser, 1938

Clevelandella volux (Walcott)

Saratogia volux WALCOTT, Smithsonian Misc. Coll., vol. 64, no. 3, p. 198, pl. 35, figs. 2, 2a, 1916.

Upper Cambrian, Eau Claire; (loc. 78a) Eau Claire, Wisconsin.

Holotype.—U.S.N.M. no. 61714.

CHUANGIA Walcott, 1911

Chuangia suni, n. sp.

Chuangia batia SUN, Pal. Sinica, ser. b, vol. 1, fasc. 4, p. 58, pl. 4, figs. 4a-c, 1924.

This species is narrower than *C. batia*. The eyes are situated somewhat more forward and are perhaps a little larger. The species

also has a wider preglabellar area. Glabellar furrows are evidently very faint.

Upper Cambrian, Kaolishanian; Pagoda Hill, Taianfu, Shantung, China.

Cotypes.—Geol. Surv. China nos. 579-583.

DEADWOODIA, n. gen.

This trilobite genus is represented by a single cranidium. However, it appears among undescribed material of Iron-ton age, from several localities and consequently description is warranted.

The cranidium is characterized by a very large, nearly quadrate glabella, highly arched in both directions and standing high above the fixigenes. Glabellar furrows essentially absent. Occipital furrow deep, but narrow. Brim is wide, concave as a whole. Preglabellar area slightly convex, dipping steeply down from the dorsal furrow. Anterior furrow shallow, with the essentially flat rim turned nearly into a horizontal position. Fixigenes narrow, as well as the postero-lateral limbs. Eyes rather large, strongly bowed, and palpebral lobes separated by deep furrows.

Genotype.—*Ptychoparia* (*Liostracus*) *panope* Walcott.

Deadwoodia panope (Walcott)

Ptychoparia (*Liostracus*) *panope* WALCOTT, Proc. U. S. Nat. Mus., vol. 13, p. 275, pl. 21, fig. 13, 1890.

Upper Cambrian, Deadwood (Iron-ton equivalent); Spring Creek Canyon, about 7 miles southwest of Rapid City, Black Hills, South Dakota.

Holotype.—U.S.N.M. no. 23856.

EHMANIA Resser, 1935

Ehmania ? *agatho* (Walcott)

Asaphiscus ? *agatho* WALCOTT, Smithsonian Misc. Coll., vol. 64, no. 5, p. 391, pl. 63, figs. 9, 9a, 1916.

Upper Cambrian, Nolichucky; (loc. 123a) Big Creek, 4 miles northeast of Rogersville, Tennessee.

Cotypes.—U.S.N.M. nos. 62819-20.

ELVINIA Walcott, 1924

Elvinia roemeri (Shumard)

Dikeloccephalus roemeri SHUMARD, Amer. Journ. Sci., 2d ser., vol. 32, p. 220, 1861.

Elvinia roemeri WALCOTT (part), Smithsonian Misc. Coll., vol. 75, no. 2, p. 56, 1924; idem, no. 3, p. 88, 1925; BRIDGE (part), U. S. Geol. Surv. Prof. Pap., 186-M, p. 251, pl. 67, figs. 2a, b, 3a, b; pl. 69, figs. 1-8, 10, 15, 1937.

E. roemeri is not a widespread species, but many other forms have been mistakenly identified with it. Without Shumard's specimens it is impossible to know which Texas species received the name *E. roemeri*. Bridge studied Roemer's original material and commented on the other species of the genus, but he failed to select a type for *E. roemeri*. Inasmuch as Shumard's types are lost and Shumard specifically states that figure 2a of Roemer is the species he was describing, it is logical to choose that specimen as the lectotype. Bridge went so far as to say that this specimen "is the nearest thing to a type that exists."

Upper Cambrian, Wilberns; $\frac{1}{2}$ mile east of Camp San Saba and (loc. 14i) 1 mile west of Cherokee, in San Saba County; (loc. 70) Morgans Creek, 8 miles northwest of Burnet, Texas.

Lectotype and paratypes.—Univ. Bonn; casts, U.S.N.M. no. 95485.

***Elvinia texana*, n. sp.**

Elvinia roemeri BRIDGE (part), in Sellards, Adkins, and Plummer, Texas Univ. Bull. 3232, p. 323, pl. 2, figs. 17, 18, 1933; BRIDGE (part), U. S. Geol. Surv. Prof. Pap. 186-M, p. 251, pl. 69, fig. 15, 1937.

This form is about the same size as *E. roemeri* but is relatively longer. The width across the fixigenes immediately in front of the eyes is less than in *E. roemeri*, and the profile is less highly arched in both directions. The glabella of *E. texana* is rather sharply truncate in front, and the anterior facial sutures extend almost straight forward.

No pygidium has been definitely assigned to this cranidium. Several are present in the collection, but only one is good enough to assign to a species. By its size and other features this pygidium seems to be more logically referred to a larger species.

Upper Cambrian, Wilberns; (loc. 68) Packsaddle Mountain, 12 miles southeast of Llano, Texas.

Holotype.—U.S.N.M. no. 93013.

***Elvinia shumardi*, n. sp.**

Elvinia roemeri WALCOTT (part), Smithsonian Misc. Coll., vol. 75, no. 2, p. 56, pl. 11, fig. 3, 1924; idem, no. 3, p. 88, pl. 17, figs. 9-13, 1925; BRIDGE (part), in Sellards, Adkins, and Plummer, Texas Univ. Bull. 3232, p. 323, pl. 2, fig. 19, 1933; BRIDGE (part), U. S. Geol. Surv. Prof. Pap. 186-M, p. 251, pl. 69, figs. 9, 10, 1937.

This is a large species, attaining an average size about twice that of *E. roemeri*. The anterior suture diverges more than *E. texana*, although the relative width immediately in front of the eyes is about the same. *E. shumardi* is decidedly flat in lateral profile. Longitudinally the species has a highly arched profile, but without being greatly curved. The neck furrow is discontinuous, a distinctive feature of the species.

It should be added that Walcott selected this species to represent Shumard's *E. roemeri*. This selection cannot stand because Roemer's figure 2a was specifically mentioned by Shumard.

Upper Cambrian, Wilberns: (loc. 70) Morgans Creek, about 8 miles northwest of Burnet; and (loc. 68) Packsaddle Mountain, 12 miles southeast of Llano, Texas.

Holotype.—U.S.N.M. no. 70259; paratypes, no. 70260, 1.

***Elvinia bridgei*, n. sp.**

Elvinia roemeri BRIDGE (part), U. S. Geol. Surv. Prof. Pap. 186-M, p. 251, pl. 60, figs. 19-21, 1937.

Unfortunately only an incomplete cranidium of this species was illustrated. Although none of the numerous cranidia in the collection are complete, many are more so than the specimen illustrated. However, this cranidium shows sufficient of the width of the head and the depth of the furrows to characterize the species. The occipital furrow is deeper and wider than shown. The eyes are in a position about parallel to the course of the dorsal furrow. The preglabellar area is bulged so that the rather straight anterior furrow is deep, and is marked by irregular longitudinal ridges. The rim is rather wide and swollen, separated by a deep anterior furrow. This species is much more highly arched longitudinally than laterally.

The associated pygidium is of normal type, and has the rim turned up rather sharply.

There are several other species of *Elvinia* in the Oklahoma collections, but, since they require illustration, are not included in this paper.

Upper Cambrian, Honey Creek: (loc. 89v) NE. $\frac{1}{4}$ Sec. 9, T. 1 S., R. 1 W., $\frac{1}{4}$ miles southeast of Hennepin, Arbuckle Mountains, Oklahoma.

Cotypes.—U.S.N.M. no. 93025.

***Elvinia missouriensis*, n. sp.**

Elvinia roemeri BRIDGE (part), U. S. Geol. Surv. Prof. Pap. 186-M, p. 2511, pl. 69, figs. 12, 13, 1937.

Bridge figured one of the two species present at the locality. The holotype is a well-preserved cranidium.

This species is characterized by its relative narrowness immediately in front of the eyes. The eyes are not parallel to the dorsal furrow, but make a wide angle with the axis. Eyelines are rather heavy. The cranidium is arched considerably laterally, this being accentuated by the pronounced downward depression of the anterior angles of the brim. Longitudinally the head is also highly arched, the greatest curvature being in the anterior half. The preglabellar area is bulged a bit and the thickened rim is sharply upturned.

Upper Cambrian, Davis; (loc. 11k) near shaft of Federal Lead Mine No. 4, Flat River, Missouri.

Holotype.—U.S.N.M. no. 93011.

***Elvinia dakotensis*, n. sp.**

Elvinia roemeri BRIDGE (part), U. S. Geol. Surv. Prof. Pap. 186-M, p. 251, pl. 69, figs. 14, 16, 1937.

This species is nearest like *E. missouriensis*, differing in the rounding of the anterior portion of the glabella and the slightly narrower width immediately in front of the eyes. *E. dakotensis* also has less rugged relief in the various portions of the brim. In *E. dakotensis* the glabella does not rise so much as the *fixigenes*, and the longitudinal curvature, which is considerable, forms a rather even curve.

The librigenes are large and wide, with a strongly curved outer margin, particularly toward the genal angle. The genal spine is short and small. The associated pygidium has an axis which stands well above the flat pleural lobes.

Upper Cambrian, Deadwood; (loc. 88a) northern part of Deadwood, Black Hills, South Dakota.

Cotypes.—U.S.N.M. no. 93024.

***Elvinia utahensis*, n. sp.**

Elvinia roemeri BRIDGE (part), U. S. Geol. Surv. Prof. Pap. 186-M, p. 251, pl. 69, fig. 22, 1937.

This species is characterized by rugged relief due to the depth of all furrows, the arching of the preglabellar area and of the *fixigenes* and the depression of the anterior angles of the brim. The eyes are large and situated rather far forward.

Upper Cambrian, Orr; (loc. 32t) Fandango Spring Canyon, east side Dugway Range, Utah.

Holotype.—U.S.N.M., no. 93026.

Elvinia matheri (Walcott)

Ptychoparia matheri WALCOTT, Smithsonian Misc. Coll., vol. 57, no. 9, p. 268, pl. 44, figs. 15-17, 1912; BRIDGE (part), U. S. Geol. Surv. Prof. Pap. 186-M, p. 254, pl. 69, fig. 11, 1937.

Upper Cambrian, Potsdam; (loc. 110) east side of Whitehall, New York.

Cotypes.—U.S.N.M. nos. 58585-7.

GENEVIEVELLA Lochman, 1936

Genevievella LOCHMAN, Journ. Pal., vol. 10, no. 1, p. 40, 1936.

Llanoaspis LOCHMAN, idem, vol. 12, no. 1, p. 80, 1938.

When this genus was established, only the genotype was known. Two species were added from Texas, and the descriptions of eleven from the Appalachians are in press; consequently this is a well-represented trilobite genus. Thus far the genus is confined to the *Crepicephalus* zone.

Llanoaspis modesta and *L. undulata* Lochman become *Genevievella*.

IRVINGELLA Ulrich and Resser, 1924

Irvingella was applied to species which differ from *Chariocephalus* in a limited degree. *Chariocephalus* has large eyes situated rather far forward. The facial suture joins the dorsal furrow anterior to the eye, by which arrangement the anterior fixigene is eliminated and the brim is caused to be a single bar not attached to the fixigenes at the anterior angles. On the other hand *Irvingella* has even larger eyes than *Chariocephalus*, the extra length being attained by the rear portion of the palpebral lobes extending farther back. At the same time the eyes are slanted outward from the axis of the head. Above all, *Irvingella* differs from *Chariocephalus* by having anterior fixigenes which unite with the brim.

Irvingella tumifrons (Hall and Whitfield)

Chariocephalus tumifrons HALL and WHITFIELD, U. S. Geol. Expl. 40th Par., vol. 4, p. 224, pl. 2, figs. 38, 39, 1877.

Upper Cambrian, Secret Canyon; Pogonip Mountain, White Pine District, Nevada.

Holotype.—U.S.N.M. no. 24561.

KOCHINA Resser, 1935**Kochina? lux (Walcott)**

Ptychoparia lux WALCOTT, Smithsonian Misc. Coll., vol. 67, no. 3, p. 90, pl. 12, fig. 5, 1917.

Lower Cambrian, Mount Whyte; (loc. 61d) southwest slope Mount Shaffer, British Columbia.

Holotype.—U.S.N.M. no. 64387.

LONCHOCEPHALUS Owen, 1852

Lonchocephalus verrucosus (Whitfield)

Conocephalites verrucosus WHITFIELD, Amer. Mus. Nat. Hist. Bull. 1, p. 146, pl. 14, figs. 9-12, 1884.

Upper Cambrian, Potsdam; near "Post office," Ausable Chasm, New York.

Cotypes.—A.M.N.H. no. 280.

MENOMONIDAE Walcott

MENOMONIA Walcott, 1916

Menomonion WALCOTT, Smithsonian Misc. Coll., vol. 64, no. 3, p. 161, 1916.

Millardia WALCOTT, idem, p. 163, 1916.

Walcott referred three genera to the Proparian family Menomonidae, but he failed to recognize that two of them were identical. Evidence for a primitive aspect about *Menomonion* and *Dresbachia* may be questioned. Evidently Walcott based his idea of this on the numerous thoracic segments of *M. calymenoides*. Examination of available specimens fails to prove that this extraordinarily long thorax belongs to *Menomonion*, although association in three instances suggests the possibility. Even if the genotype has 42 thoracic segments, one can hardly consider this alone as evidence of primitive structure.

It seems rather that the Menomonidae are a highly specialized group descended from species now placed in *Alokistocare*.

Menomonion is a characteristic trilobite of the early Upper Cambrian *Cedaria* zone; thus far being confined to that zone. Whitfield's original specimens of the type species are on small pieces of rock with the types of *Cedaria woosteri*.

Millardia was distinguished from *Menomonion* by differences of brim and in having fewer thoracic segments. There is a difference in the brim of *M. calymenoides* and of *M. semic* but it involves no altered structure and the gap between the two species is bridged by intermediate forms. *M. calymenoides* has a much swollen brim, whereas other species obtain the same rigidity by arching the short brim. Many specimens referred to *Millardia* retain the librigenes, giving them a different aspect, which caused their reference to a separate genus.

Dresbachia is a distinct, but closely related genus. Compared with *Menomonion*, the glabella is essentially the same but the fixigenes are

much larger. The large librigenes—the part of this trilobite most commonly preserved—are attached to a very short brim, which is reduced to little more than a line, terminating in a swollen knob like the rim *Menomonina*. In other words *Dresbachia* is characterized by the lateral shortening of the preglabellar area to a mere line for the attachment of the librigenes which lies wholly in front of the glabella.

Besides the genotype and the species formerly referred to *Millardia*, several new species from the Appalachian Nolichucky formation are in press.

***Menomonina avitas* (Walcott)**

Millardia avitas WALCOTT, Smithsonian Misc. Coll., vol. 64, no. 3, p. 165, pl. 28, figs. 5-5e, 1916.

Upper Cambrian, Warrior; (loc. 107k) 2 miles north of Benore, Center County, Pennsylvania.

Holotype.—U.S.N.M. no. 61629.

***Menomonina magnagranulata* (Lochman)**

Millardia magnagranulata LOCHMAN, Journ. Pal., vol. 12, no. 1, p. 84, pl. 18, fig. 3, 1938.

Upper Cambrian, Cap Mountain; southwest side of Lion Mountain, Highway 29, 9 miles northwest of Burnet, Texas.

Holotype.—U.S.N.M. no. 95015.

***Menomonina optata* (Hall)**

Conocephalites optatus HALL, 16th Ann. Rep. New York State Cab. Nat. Hist., p. 222, pl. 5A, fig. 7, 1863. Trans. Albany Inst., vol. 5, p. 195, 1867.

Ptychoparia optata MILLER, North Amer. Geol. Pal., p. 539, 1889.

Millardia optata WALCOTT, Smithsonian Misc. Coll., vol. 64, no. 3, p. 165, pl. 28, figs. 4, 4a-f, 1916.

One cannot be certain that Hall's original type and the specimens figured by Walcott represent the same species. At any rate Hall's original is a very small specimen.

Upper Cambrian, Eau Claire; Willow River Falls, Trempealeau, and other localities in Wisconsin and Minnesota.

Holotype.—A.M.N.H. no. 322; plesiotypes, U.S.N.M. nos. 61626-8.

***Menomonina semele* (Walcott)**

Millardia semele WALCOTT, Smithsonian Misc. Coll., vol. 64, no. 3, p. 166, pl. 28, figs. 3-3c, 1916.

Upper Cambrian, Weeks; (loc. 30 n) Weeks Canyon, House Range, Utah.

Cotypes.—U.S.N.M. nos. 61622-5.

Menomonion texana, n. sp.

Millardia avitas LOCHMAN (not Walcott), Journ. Pal., vol. 12, no. 1, p. 84, pl. 18, figs. 4-5, 1938.

This species evidently was referred to *M. avitas* because it has smaller granules than *M. magnagranulata*. The reference to the Pennsylvania species cannot stand. *M. avitas* has a few scattered large granules on the glabella and fixigenes; the remainder of the cephalon is smooth to finely granulose or ornamented with lines. The eyes of *M. avitas* are elevated on rather long stalks. This may also have been the case in *M. texana* as the eyes are broken off. *M. texana* is further characterized by a long slender glabella and the eyes are rather far forward.

Upper Cambrian, Cap Mountain; southwest side Lion Mountain, Highway 29, 9 miles northwest of Burnet, Texas.

Holotype.—Mount Holyoke Mus. no. 655; paratype, no. 656.

Menomonion lochmanae (Lochman)

Millardia avitas LOCHMAN, Journ. Pal., vol. 12, no. 5, p. 469, pl. 56, figs. 27, 28, 1938.

This species differs from *M. avitas* in the more incurved anterior margin and considerably larger fixigenes.

Upper Cambrian, Petit Jardin; Cape St. George, Newfoundland.

Holotype.—Yale Peabody Mus. no. 15822.

NORWOODIA Walcott, 1916

Norwoodia WALCOTT, Smithsonian Misc. Coll., vol. 64, no. 3, p. 168, 1916.

Whitfieldina RESSER, idem, vol. 95, no. 22, p. 27, 1937.

Just after the 1937 paper appeared, the genus *Norwoodia* was reconsidered in conjunction with studies in the southern Appalachians. As soon as the extraneous species then in *Norwoodia* were removed, it became clear that *Whitfieldina* is not a valid genus, because its type species is a typical *Norwoodia*, contrary to the misleading published figures.

Norwoodia quadrata (Whitfield)

Conoccephalites quadratus WHITFIELD, Ann. Rep. for 1879, Wisconsin Geol. Surv., p. 47, 1880; Geol. Wisconsin, vol. 4, p. 180, pl. 1, figs. 15, 16, 1882.

Whitfieldina quadrata RESSER, Smithsonian Misc. Coll., vol. 95, no. 22, p. 27, 1927.

Upper Cambrian, Eau Claire; Eau Claire and other localities in Wisconsin.

Cotypes.—Univ. Wisconsin.

OLENOIDES Meek, 1877

Olenoides expansus (Walcott)

Dicelloccephalus ? *expansus* WALCOTT, U. S. Geol. Surv. Mon. 8, p. 45, pl. 9, fig. 19, 1884.

Dolichometopus ? *expansus* WALCOTT, Smithsonian Misc. Coll., vol. 64, no. 5, p. 368, pl. 53, figs. 5, 5a, 1916.

Middle Cambrian, Eldorado; (loc. 35b) east slope Prospect Mountain, Eureka District, Nevada.

Holotype.—U.S.N.M. no. 15450.

ORYCTOCEPHALUS Walcott, 1886

Species of this genus have not been carefully discriminated, and specific names were very carelessly used. A brief revision clears the way for erection of the necessary new species.

Oryctocephalus, as now constituted, contains two groups of species. The valid species previously recognized are listed under the two groups.

Group of <i>O. primus</i> (genotype)	<i>O. walcotti</i> Resser
<i>O. primus</i> Walcott	<i>O. salteri</i> Reed
<i>O. burgessensis</i> , n. sp.	<i>O. indicus</i> (Reed)
<i>O. walkei</i> Matthew	<i>O. kobayashi</i> Saito
Group of <i>O. reynoldsi</i>	<i>O. orientalis</i> Saito
<i>O. reynoldsi</i> Reed	<i>O. saitoi</i> , n. sp.

In addition, one undescribed species of the *O. primus* group and several of the *O. reynoldsi* group are in hand.

Oryctocephalus burgessensis, n. sp.

Oryctocephalus primus KOBAYASHI, Journ. Faculty Sci. Imp. Univ. Tokyo, sec. 2, vol. 4, pt. 2, p. 147, pl. 15, fig. 1, 1935.

Kobayashi picked up a photograph in the National Museum collections and published it as *O. primus*, but this illustration was prepared by Walcott because he recognized that it was not *O. primus*.

O. burgessensis is the most abundant species of the genus in the Burgess shale. It is characterized by a normal cranidium, seven thoracic segments, and slender pygidial spines of even length. The rear segments of the pygidium are turned back practically parallel to the axis. The pygidial spines of even length cause this species to look much like *O. walkei*, but the rear pygidial segments are turned back more sharply.

Middle Cambrian, Burgess; (loc. 35k) Burgess Pass, near Field, British Columbia.

Holotype.—U.S.N.M. no. 96487.

Oryctocephalus indicus (Reed)

Zacanthoides indicus REED, Mem. Geol. Surv. India, Pal. Ind., ser. 15, vol. 7, p. 9, pl. 1, fig. 15, 1910.

Oryctocephalus cf. *reynoldsi* REED, idem, p. 12, pl. 1, figs. 22-24, 1910.

Reed recognized the generic position of the cranidium but referred the pygidium to *Zacanthoides*. Since both come from the same bed, at the same place, they can be regarded as representing one species.

O. indicus is chiefly distinguished from *O. salteri*, which occurs in beds at least 400 feet higher in the section, by the longer pygidial axis with proportionate reduction of the pleural lobes.

Middle Cambrian (horizon 2) : Parahio Valley, Spiti, India.

Cotypes.—Geol. Surv. India plastotypes, U.S.N.M. no. 96489.

Oryctocephalus saitoi, n. sp.

Oryctocephalus cf. *reynoldsi* SAITO, Japanese Journ. Geol. Geogr., vol. 11, no. 3, p. 232, pl. 27, figs. 16-20, 1934.

Saito recognized the distinctness of this species from *O. reynoldsi* and *O. orientalis*. He pointed out that it has one more pair of glabellar furrows than in *O. reynoldsi*.

Middle Cambrian, *Ptychoparia* beds ; near Hwangju, Hwanghaido, Chosen.

Cotypes.—Geol. Inst. Imp. Univ. Tokyo nos. 513, 516, 574.

Oryctocephalus walcotti Resser

Oryctocephalus walcotti RESSER (part), Smithsonian Misc. Coll., vol. 97, no. 3, p. 9, pl. 1, fig. 23, 1938.

In the description of this species a cranidium of *Oryctocara geikiei* was mistakenly assigned to it. The description was written before the genus was studied ; consequently, the fact that much better material is available from the Spence shale was overlooked.

Middle Cambrian, Lakeview ; (loc. 37n) Lakeview, Pend Oreille Lake, and Spence ; (loc. 55c) 5 miles southwest of Liberty, Idaho.

Holotype.—U.S.N.M. no. 95038.

PARABRISCOIA Kobayashi, 1935**Parabriscoia flabellifera (Hall and Whitfield)**

Dikellocephalus flabellifer HALL and WHITFIELD, U. S. Geol. Expl. 40th Par., vol. 4, p. 227, pl. 2, figs. 29-30, 1877.

Upper Cambrian, Secret Canyon? ; west side Pogonip Mountain, White Pine District, Nevada.

Holotype.—U.S.N.M. no. 24569.

PTARMINGIA Raymond, 1928**Ptarmingia longula, n. sp.**

Bathyuriscus cf. *rossensis* WALCOTT, Smithsonian Misc. Coll., vol. 67, no. 2, p. 49, pl. 5, figs. 6, 6a, 1917.

This species has a longer head than *P. rossensis*. The glabella is long, expanding only a little; eyes larger and prominent. A few widely scattered granules occur on the elevated portions of the test but appear to be much more numerous on exfoliated specimens.

The associated pygidium is very highly arched transversely and has a rather even border, with a large spine at the anterior angles.

Middle Cambrian, Ptarmigan; (loc. 63m') 1 mile east of Hector, south slope Mount Bosworth, British Columbia.

Holotype.—U.S.N.M. no. 63734; paratype, no. 63735.

PTEROCEPHALIA Roemer, 1849**Pterocephalia multincta (Hall and Whitfield)**

Dicellocephalus multinctus HALL and WHITFIELD, U. S. Geol. Expl. 40th Par., vol. 4, p. 226, pl. 2, fig. 37, 1877.

Pterocephalia sanctisabae BRIDGE (part), U. S. Geol. Surv. Prof. Pap. 186-M, p. 249, pl. 68, figs. 37, 38, 1937.

Upper Cambrian, Secret Canyon; Eureka District, Nevada.

Holotype.—U.S.N.M. no. 24640; plesiotype, no. 93021.

Pterocephalia laticeps (Hall and Whitfield)

Conocephalites (Pterocephalus) laticeps HALL and WHITFIELD, U. S. Geol. Expl. 40th Par., vol. 4, p. 221, pl. 2, figs. 4-7, 1877.

Pterocephalia sanctisabae BRIDGE (part), U. S. Geol. Surv. Prof. Pap. 186-M, p. 248, pl. 68, figs. 40-43, 1937.

Upper Cambrian, Secret Canyon; west side of Pogonip Mountain, White Pine District, Nevada.

Cotypes.—U.S.N.M. nos. 24562, 24561, 24579.

Pterocephalia dakotensis, n. sp.

Pterocephalia sanctisabae BRIDGE (part), U. S. Geol. Surv. Prof. Pap. 186-M, p. 246, pl. 68, figs. 27-30, 32-36, 39, 1937.

This species averages about the same size as the largest specimens of *P. sanctisabae*. It is characterized by rather large eye lobes, set nearly parallel with the axis. The pygidium is ovate, partly flattened in the shaly matrix.

P. dakotensis has a less flaring course of the anterior facial suture than *P. sanctisabae*, the eyes are more nearly parallel to the axial line

of the head, and are larger. The course of the pygidial furrows is also more evenly curved and the border is wider behind the axis.

Upper Cambrian, Deadwood; Whitewood Canyon, Deadwood, Black Hills, South Dakota.

Cotypes.—Univ. Iowa; U.S.N.M. no. 93020.

***Pterocephalia bridgei*, n. sp.**

Pterocephalia sanctisabae BRIDGE (part), U. S. Geol. Surv. Prof. Pap. 186-M, p. 246, pl. 68, figs. 25, 26, 1937.

This species is characterized by a wide brim, a relatively long glabella, and the curved course of the anterior facial suture. The pygidium assigned to the species has a narrower border than *P. sanctisabae*, and its rear margin is notched. The surface of the cranium behind the eyelines and on the glabella, is nearly smooth. Anterior to these parts the irregular longitudinal folds are rather heavy, and the surface is marked by the usual horizontal, anastomosing lines.

Upper Cambrian, Davis; (loc. 11k) near shaft Federal Lead mine no. 4, Flat River, Missouri.

Holotype and paratype.—U.S.N.M. no. 93019.

***Pterocephalia oriens*, n. sp.**

Pterocephalia sanctisabae BRIDGE (part), U. S. Geol. Surv. Prof. Pap. 186-M, p. 246, pl. 68, fig. 24, 1937.

Associated with *P. bridgei* is another, possibly smaller, species characterized particularly by its highly elevated palpebral lobes. The eyes are large, and the eyelobes are sharply separated by a deep furrow. The surface is ornamented similarly to *P. bridgei* except that the anastomosing lines are heavier.

Upper Cambrian, Davis; (loc. 11k) near shaft Federal Lead mine no. 4, Flat River, Missouri.

Cotypes.—U.S.N.M. no. 96485.

***Pterocephalia potosiensis*, n. sp.**

Pterocephalia sanctisabae BRIDGE (part), U. S. Geol. Surv. Prof. Pap. 186-M, p. 246, pl. 68, fig. 23, 1937.

Only a few specimens were obtained in a rather large collection, so that this species seems to be rare. The presence of a large librigena may be interpreted as indicating that *P. potosiensis* grew to a much larger size than the holotype indicates, or that there is more than one species present.

P. potosiensis has a wider and longer brim than other Missouri species, but it is shorter than that of *P. bridgei*. The new species is

characterized particularly by well-developed anastomosing lines on the glabella and librigenes.

Upper Cambrian, Davis; (loc. 11e) southwest of Potosi, Missouri.
Holotype.—U.S.N.M. no. 93018.

***Pterocephalia ulrichi*, n. sp.**

Pterocephalia sanctisabae BRIDGE (part), U. S. Geol. Surv. Prof. Pap. 186-M,
p. 246, pl. 68, figs. 19, 21, 1937.

This is a large, wide species with a wide flaring brim. In fact, this is the widest species thus far found. The glabella is wide and rounded in front. Likewise the anterior margin of the cranidium is more rounded than in most species. The dorsal furrow is both wide and deep, so that the glabella and cheeks next to it have considerable relief.

The pygidium is rather wide, the border of moderate width and the rear margin evidently not notched.

Upper Cambrian, Honey Creek; (loc. 9q) 15 miles northwest of Fort Sill, and (loc. 91L²) northeast of Big Baldy, Wichita Mountains, Oklahoma.

Holotype.—U.S.N.M. no. 93016; paratype, no. 93014.

***Pterocephalia silvestris*, n. sp.**

Pterocephalia sanctisabae BRIDGE (part), U. S. Geol. Surv. Prof. Pap. 186-M,
p. 246, pl. 68, fig. 20, 1937.

This is also a wide form and has a very large brim. Compared with *P. ulrichi*, the brim is longer and the dorsal and glabellar furrows shallower.

Upper Cambrian, Honey Creek; (loc. 91a) 4 miles southeast of Hennepin, West Timbered Hills, Arbuckle Mountains, Oklahoma.

Holotype.—U.S.N.M. no. 93015.

***Pterocephalia deckeri*, n. sp.**

Pterocephalia sanctisabae BRIDGE (part), U. S. Geol. Surv. Prof. Pap. 186-M,
p. 246, pl. 68, figs. 22, 31, 1937.

This species is particularly wide opposite the front end of the glabella. The eyelines are heavy and the eyes prominent by reason of their upturned position, but the palpebral lobes slope up only moderately. The surface is highly ornamented in the usual fashion, but the anastomosing lines on the glabella and fixigenes have such a fine mesh that the surface appears to be granulated.

The pygidium is rather narrow and high.

Upper Cambrian, Honey Creek; (loc. 89v) 4 miles south of Hennepin, west Timbered Hills, Arbuckle Mountains, Oklahoma.

Holotype.—U.S.N.M. no. 93017.

PTEROCEPHALINA, n. gen.

For many years the genotype has been referred from one genus to another, which, besides those listed below, include *Anomocare*, *Niobe*, *Saukia*, and *Platycolpus*. The pygidium resembles that of both *Pterocephalia* and the Saukinae but does not fit into either. Careful search of the collections has revealed a partial cranidium which also has affinities with *Pterocephalia* but cannot be placed in that genus.

Pterocephalina is characterized by a broad bordered pygidium in which the wide doublure is almost severed by the deep notch in the rear margin of the tail. The axis, which is subcylindrical, extends almost to this notch, being connected with it by a sharp postaxial ridge. Unexfoliated specimens show that pleural fusion is far advanced, but the furrows are traceable on the upper surface nearly to the border. The holotype shows the underside and hence the extent of the doublure, but not the pleural furrows.

The cranidium assigned to the species is incomplete. It consists of a large prominent, highly arched glabella, on which the rear pair of furrows are represented by slight, rearward directed indentations. Eyelines present. Eyes evidently of moderate size. Fixigenes less than half glabellar width. Brim very wide, apparently with a flat, sharply upturned rim. Wide preglabellar area is striated by coarse irregular lines among which are interspersed scattered lumps. The entire cranidium is highly arched in both directions.

Genotype.—*Dikellocephalus bilobatus* Hall and Whitfield.

***Pterocephalina bilobata* (Hall and Whitfield)**

Dikellocephalus [*Pterocephalus*] *bilobatus* HALL and WHITFIELD, U. S. Geol.

Expl. 40th Par., vol. 4, p. 226, pl. 2, fig. 36, 1877.

Dicelloccephalus bilobatus WALCOTT, U. S. Geol. Surv. Mon. 8, p. 40, 1884.

Platycolpus bilobatus WALCOTT, Smithsonian Misc. Coll., vol. 57, no. 13, p. 340, 1914.

Upper Cambrian, Secret Canyon; (loc. 65) east side Sierra Canyon, opposite Pinnacle Peak, and (loc. 61) south of Hamburg Mine, Eureka District, Nevada.

Holotype.—U.S.N.M. no. 24568.

SAUKIELLA Ulrich and Resser, 1933**Saukiella junia (Walcott)**

Saukia junia WALCOTT, Smithsonian Misc. Coll., vol. 57, no. 13, p. 378, text fig. 17, 1914.

Upper Cambrian, Signal Mountain; (loc. 12j) 2 miles southwest of Signal Mountain, Wichita Mountains, Oklahoma.

Holotype.—U.S.N.M. no. 60677.

SINOSAUKIA Sun, 1935**Sinosaukia bella (Walcott)**

Ptychaspis bella WALCOTT, Proc. U. S. Nat. Mus., vol. 30, p. 585, 1906; Research in China, vol. 3, Carnegie Inst. Publ. 54, p. 180, pl. 17, fig. 9, 1913.

Upper Cambrian, Fengshan; (loc. C 74) east of Fang-lan-chon, Shansi, China.

Holotype.—U.S.N.M. no. 58124.

TELLERINA Ulrich and Resser, 1933**Tellerina rustica (Walcott)**

Saukia rustica WALCOTT, Smithsonian Misc. Coll., vol. 57, no. 13, p. 383, text figs. 18-19a, 1914.

Upper Cambrian, Signal Mountain; (loc. 12j) 2 miles southwest of Signal Mountain, Wichita Mountains, Oklahoma.

Holotype.—U.S.N.M. no. 60678; paratypes, nos. 60679-80.

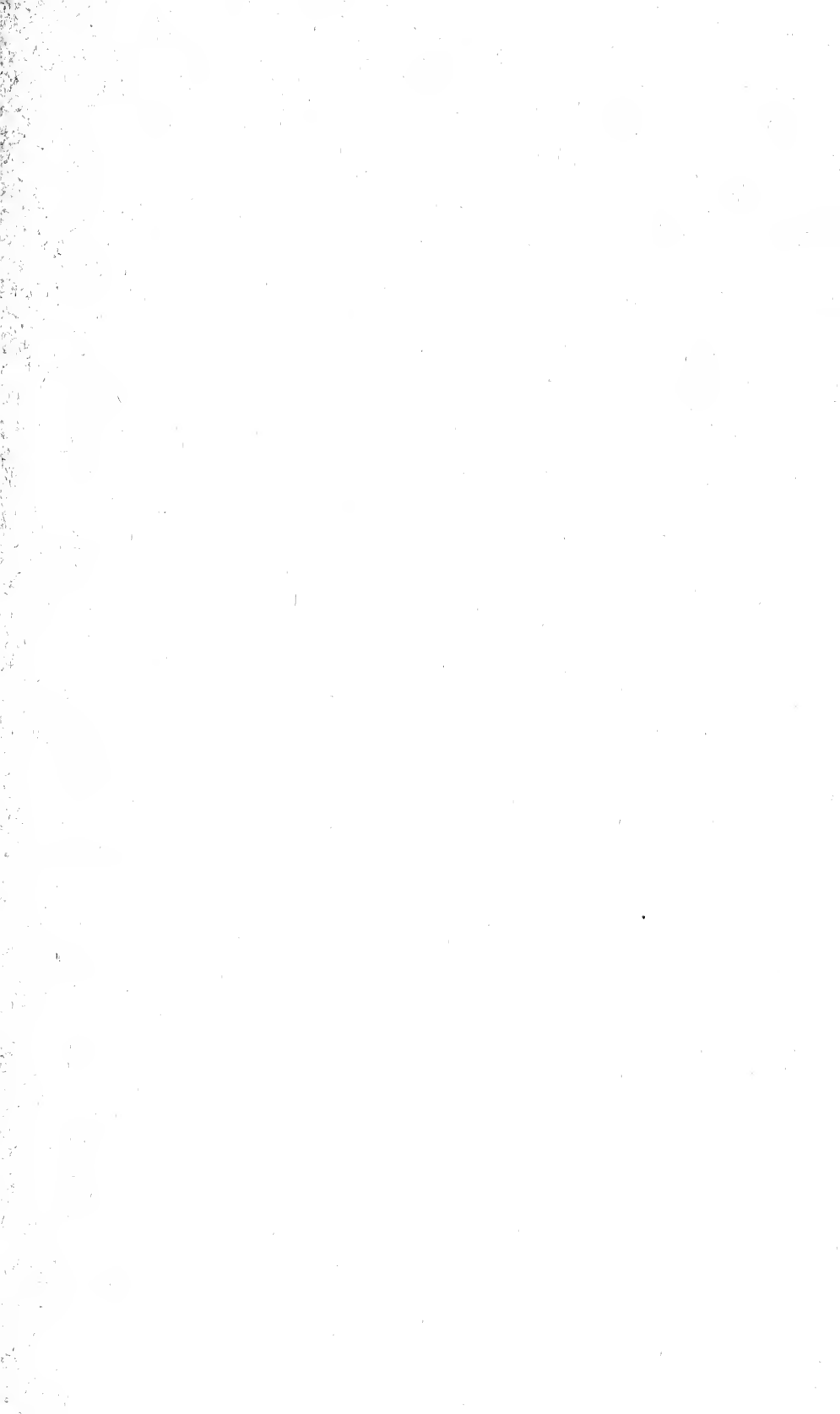
TONKINELLA Mansuy, 1916**Tonkinella kobayashi, new name.**

Tonkinella breviceps KOBAYASHI, Journ. Faculty Sci. Imp. Univ. Tokyo, sec. 2, vol. 4, pt. 2, p. 150, pl. 15, figs. 6, 8, 9, 1935.

This name was previously used for a species in Kashmir.

Middle Cambrian, Taiki; Neietsu, south Chosen.

Cotypes.—Geol. Inst. Imp. Univ. Tokyo.





SMITHSONIAN MISCELLANEOUS COLLECTIONS

VOLUME 97, NUMBER 11

AN ASSAY METHOD FOR GROWTH-PROMOTING
SUBSTANCES UTILIZING STRAIGHT GROWTH
OF THE AVENA COLEOPTILE

(WITH ONE PLATE)

BY

ROBERT L. WEINTRAUB

Division of Radiation and Organisms,
Smithsonian Institution



(PUBLICATION 3488)

CITY OF WASHINGTON

PUBLISHED BY THE SMITHSONIAN INSTITUTION

DECEMBER 31, 1938

SMITHSONIAN MISCELLANEOUS COLLECTIONS
VOLUME 97, NUMBER 11

AN ASSAY METHOD FOR GROWTH-PROMOTING
SUBSTANCES UTILIZING STRAIGHT GROWTH
OF THE AVENA COLEOPTILE

(WITH ONE PLATE)

BY

ROBERT L. WEINTRAUB

Division of Radiation and Organisms,
Smithsonian Institution



(PUBLICATION 3488)

CITY OF WASHINGTON
PUBLISHED BY THE SMITHSONIAN INSTITUTION
DECEMBER 31, 1938

The Lord Baltimore Press
BALTIMORE, MD., U. S. A.

AN ASSAY METHOD FOR GROWTH-PROMOTING SUBSTANCES UTILIZING STRAIGHT GROWTH OF THE AVENA COLEOPTILE

By ROBERT L. WEINTRAUB

Division of Radiation and Organisms, Smithsonian Institution

(WITH ONE PLATE)

The most delicate available methods for the determination of plant growth-promoting substances involve the direct measurement of the effects of these substances on the growth of suitable plant test objects. The most commonly employed indicator is the decapitated *Avena* coleoptile. Two general techniques are available; one makes use of the elongation (straight growth) resulting from the application of the substance in question symmetrically with respect to the long axis of the coleoptile, the other utilizes the curvature produced by unilateral application of the growth-promoting substance. The latter method, which has been more widely used, has been described repeatedly (see *e. g.*, Boysen-Jensen, 1936; Went and Thimann, 1937; Avery, Burkholder, and Creighton, 1937) and need not be detailed here. As Went and Thimann (1937, p. 51) point out, "The convenience of curvature methods rests upon two facts: (1) the residual growth, after decapitation, is the same on both sides of the plant and thus is automatically eliminated from the measurement—no controls are necessary; and (2) only one measurement need be made; there is no zero reading." It should be noted, however, that the first condition, namely, the uniformity of the residual growth, is true only during the first 2 hours following decapitation (cf. fig. 20, Went and Thimann, 1937), and this limits the length of the test period.

Thus the curvature test measures not the maximum amount of curvature (growth) which can be induced by the applied substance, but rather the mean rate of curvature during a given period. During this period the rate is not constant and may even change in sign (cf. Schneider and Went, 1938). The factors which cause a reduction in the curvature rate and therefore in the amount of curvature at the end of the test period are: (1) gravity, which causes a geotropic curvature in the opposite direction; (2) the effect of "physiological regeneration" of the tip, and (3) the lateral transport of the applied growth-

promoting substance across the coleoptile, producing a growth acceleration on the far side of the plant. The influence of the last-named factor is very marked in the case of a number of substances which show relatively little or no activity by the curvature method but have considerable effect on straight growth (cf. table XII, pp. 137-139, Went and Thimann, 1937). This lateral transport is greater the higher the concentration of growth-promoting substance applied; the net result is a decrease in the sensitivity of the test.

Methods employing straight growth have been employed occasionally but have not come into routine usage, largely because of the inconvenience in measuring the growth. The present report describes an assay procedure utilizing straight growth of the coleoptile of *Avena sativa*,¹ in which the sensitivity of the response and the ease and accuracy of measurement are at least as great as in the commonly used curvature test. In addition, the method offers a number of other technical advantages.

The procedure will be outlined briefly first, and then each step will be discussed in greater detail.

SUMMARY OF METHOD

Seeds are planted on agar slants in small test tubes at a determined distance below the rim of the tube. The seedlings are germinated and grown under controlled conditions. When the coleoptiles have attained a given length they are decapitated level with the rim of the tube and the leaf is withdrawn completely. Blocks of agar, containing the growth-promoting substance to be tested, are placed terminally upon the entire cut surface of the stump. After some time a shadow-graph is made in the usual manner. The length of the coleoptile which extends above the rim of the tube represents the growth increment during the test period. It can be measured very easily with a dissecting microscope equipped with an ocular micrometer.

TEST TUBES AND RACKS

Soft glass or Pyrex tubes having an inner diameter of about 15 mm and a length of 7 cm have been found satisfactory. Trials with larger tubes indicate that within reasonable limits the size is immaterial. A simple rack for the tubes may be constructed by boring a row of holes in a wood block. The holes should be of such depth and

¹ *Avena sativa* var. Markton has been used exclusively. The seeds were obtained through the courtesy of Mr. T. Ray Stanton, of the U. S. Department of Agriculture.

diameter that the tubes slip in easily and stand upright: 2.5 cm between centers allows sufficient room to manipulate the tubes. The length of the block, of course, determines the number of tubes and will depend upon the size of the photographic paper, incubator, etc., which one uses. For ready identification of the racks and the shadow-graphs some suitable design (*e. g.*, a letter or number) may be punched or drilled in a strip of sheet metal which is fastened against the back of the rack (see pl. 1). Machine-made test tubes usually have sufficiently uniform rims; if the tubes are made by hand from glass tubing it is necessary to grind the rim at right angles to the long axis of the tube. A mark should be made on the tube at a given distance below the rim; if it is desired to change the depth of planting in different experiments a glass-marking pencil is convenient; otherwise, a scratch made with a file or carborundum wheel furnishes a permanent mark.

THE AGAR SLANT

The same purified agar which is used for the test blocks is suitable. The concentration of agar should not be less than 0.8 percent. Greater concentrations, up to 2 percent, give equally good results; 0.9 to 1 percent agar has been routinely used. The agar may be made up in nutrient solution if desired but tap or distilled water have given uniformly satisfactory results. The growth rate of the coleoptile will be found to depend upon the composition of the agar. The simple device used in bacteriological laboratories is very convenient for filling the tubes with the melted agar. This consists of a funnel connected by a short length of rubber tubing to a glass tip and provided with a pinch clamp. The tubes are placed in the rack, filled up to the mark and the whole rack is tilted backward through about 60° so that the agar solidifies in a slant. The angle of the slope (and of the planted seed) should be such that the coleoptile grows erect without being required to curve. One hundred tubes can be charged with agar in about 8 minutes.

PLANTING AND GERMINATING SEEDS

The husked seed is pressed gently against the surface of the agar slant with the groove side down and the embryo at the level of the mark on the tube. The seeds may be soaked in water before planting or planted without previous soaking. Soaking does not affect the growth rate or the sensitivity of the plants. Furthermore, husked seeds planted dry on the agar absorb water nearly as rapidly as

if they are immersed in water, so that there is no advantage in preliminary soaking. Planting of dry seeds obviates a second handling of the seedlings. Under the conditions routinely employed in this laboratory (growth continuously from the time of planting in red light (Wratten Safelight, series o) at 25° C. and about 90 percent relative humidity) the coleoptiles attain a length of 25 mm at about 65 hours after planting. The growth rate at this time, and for the next 24 hours, is approximately 0.9 mm per hour. Plants grown on agar slants in small tubes as described have shown less individual variability than those handled in any other way, as on filter paper, or sand, in the usual glass *Avena* holders, or on porous stone wicks. One hundred seeds can be planted in the tubes in about 10 minutes.

LENGTH OF COLEOPTILE

In connection with the size of the coleoptile used for the test, three factors have been studied. These are the total length of coleoptile, the length of the tip decapitated, and the length of the stump used.

The growth rate of the basal portion of the coleoptile decreases as the total length of the coleoptile increases, and if 20 to 25 mm of the coleoptile tip are removed, the stump makes practically no growth when a plain agar block is applied. If coleoptiles are used under these conditions no controls are necessary. However, the sensitivity (used here as the amount of growth in excess of the control which is produced by application of a given amount of growth substance) of the basal portion also decreases rather rapidly as the total length of the coleoptile increases. The 20-mm stumps of 40-mm coleoptiles have practically no residual growth under the conditions of the test, but do have a rather high sensitivity. It is possible, therefore, to use coleoptiles of this length without controls. More commonly, however, 13-mm stumps of 24- to 27-mm coleoptiles have been used because the plants are ready for the test nearly a day earlier. A control set must, of course, be included.

It is not intended to suggest that it is necessary to employ plants of just this length or even that the described conditions are optimal, but merely to indicate the technique which has given satisfactory results. As a matter of fact, since the test is essentially comparative, a few millimeters variation in the length of the test plants is of no consequence provided the plants are randomized throughout the different sets.

DECAPITATION

It is essential that the cut surface of the coleoptile be exactly at the level of the test tube rim and that the cut be clean and horizontal (at right angles to the long axis of the coleoptile). Otherwise the plants may bend and measurement will be difficult. Decapitation can be performed quite rapidly by making a small cut partially through one (or two opposite) sides of the coleoptile with a thin safety razor blade held flat against the rim of the tube and bending the coleoptile toward the cut with the fingers or forceps until it breaks. The leaf is pulled out completely. It is often possible to break off the coleoptile and withdraw the leaf in a single motion. One hundred coleoptiles can be decapitated in 30 minutes or less.

AGAR TEST BLOCKS

In the development of the method, weighed amounts of dehydrated agar were mixed with aqueous solutions of known concentrations of indole-3-acetic acid, or of auxin-a.² Similar results have been obtained with both of these growth-promoting substances. The test blocks were prepared with an apparatus similar to that described by DuBuy (1938).

Thimann and Schneider (1938) have reported that the concentration of agar in the test blocks is of considerable importance in the *Avena* curvature test. In general they found that a given concentration of indole-3-acetic acid produced larger curvatures the lower the agar concentration. Similar, although less marked, differences have been found in the present study of straight growth. The use of 1.5 percent agar has been adopted as a general procedure.

SIZE OF TEST BLOCKS

Went (1928) concluded that with 0.9 mm³ blocks the curvatures are proportional to the absolute amount of growth substance in the blocks. Van der Weij (1931) and Thimann and Bonner (1932) concluded that the curvatures are proportional to the concentration of growth substance in the block. The data of Thimann and Bonner indicate that the rate at which the growth substance passes from the block to the plant is proportional to its concentration in the block at any moment. The change in concentration of growth substance in the block during any given period will be less the greater the volume of

² A solution of pure crystalline auxin-a was very generously supplied by Prof. F. Kögl, of the University of Utrecht.

the block. Therefore the larger the block the longer the time during which the induced growth will be proportional to the original concentration of applied growth substance. Much larger blocks can be applied terminally than can be applied unilaterally.

With blocks as large as 26 mm³ it has been found that the straight growth rate of the decapitated coleoptiles remains constant for at least 6 hours. As blocks of this size can be manipulated very conveniently they have been adopted.

The test blocks are applied so as to cover the entire cut surface of the coleoptile stump. A small drop of water or gelatin solution may be previously applied to the cut surface in order to insure good contact with the block. About 20 minutes are required for the application of 100 blocks.

Schneider and Went (1938) have shown that the length of time between decapitation and application of the blocks is of considerable importance in the curvature test. This has been confirmed by Thimann and Schneider (1938). In the straight growth method, on the other hand, the response to applied growth substance has not been found to be significantly influenced by the interval between decapitation and application of the blocks, at least within the limits of 5 to 120 minutes.

LENGTH OF TEST PERIOD

The greatest sensitivity is obtained with the longest test period during which the growth in excess of the control is proportional to the concentration of applied growth-promoting substance. That is, under such conditions the absolute useful amount of growth is the greatest, and consequently the measurement can be made with greatest accuracy. Actually, it has been found that a test period of 3 to 4 hours is quite adequate. In the present study a 4-hour period has been generally used. In practice it is not essential to use a test period of any exactly predetermined length. Hence, if it is inconvenient to terminate the test at precisely 4 hours, there is no objection to making the test period several minutes shorter or longer. In any comparable series, of course, the test periods for all the sets should be the same.

ENVIRONMENTAL CONDITIONS OF TEST

Thimann and Schneider (1938) have reported that the growth response of coleoptile sections to indole-3-acetic acid depends upon the conditions of illumination of the seedlings during the previous development; maximal response was found when the plants received red light during the first several hours of germination and were kept

in darkness thereafter. It has not been determined whether this is true also of the coleoptile stumps attached to the seeds as employed in the present technique. As has been mentioned previously, constant illumination with red light has been used, since this permits absolute reproducibility in successive lots of plants and is much more convenient when successive lots are grown concurrently in a single dark room. It has been found, however, that the sensitivity is not appreciably different whether the plants are kept in darkness or given red light during the test period itself.

With an adequate water supply to the roots of the plants, considerable differences in atmospheric humidity do not influence the sensitivity. No significant difference in growth rate was found between plants at 100 percent and at 75 percent relative humidity even though the test blocks shrink very considerably at the lower humidity.

MEASUREMENT OF GROWTH

For measurement of the shadowgraphs a dissecting microscope equipped with a $14\times$ ocular and a $2\times$ objective has been used. The ocular is provided with a 1-cm scale subdivided into 100 divisions. One mm on the scale (10 divisions) corresponds to 0.5 mm on the shadowgraph so that the length can be read directly to 0.05 mm. The uncertainty in measuring is of the order of one scale division. Since the growth of the control plants in four hours is about 0.7 mm, this corresponds to an error of about 7 percent; in the test plants, which make more growth, the error of measurement is correspondingly reduced. Furthermore, the error tends to be minimized when the average of a number of plants is taken.

RESULTS

The usefulness of the *Avena* coleoptile as a test object rests upon the fact that the induced growth is proportional, within certain limits, to the concentration of applied growth-promoting substance. That such a proportionality does exist was demonstrated by Thimann and Bonner (1933), and has been confirmed repeatedly in the present study. Figure 1 represents the relationship between growth and growth substance concentration which has been found with the procedure here employed. It will be seen that the curve is a typical Blackman curve with a very short transition region, very similar to that obtained originally by Went (1928) for the curvature test. The work of Thimann and Schneider (1938) indicates that, in the curvature test

at least, the form of the curve may vary greatly according to the technique used. No evidence of a similar situation in the straight growth response has been obtained as yet.

DISCUSSION

In addition to the theoretical preferability of utilizing straight growth rather than curvature, the present method offers several technical advantages. The usual glass holders, which are time-consuming to make, difficult to clean and easily broken, are eliminated. The solid

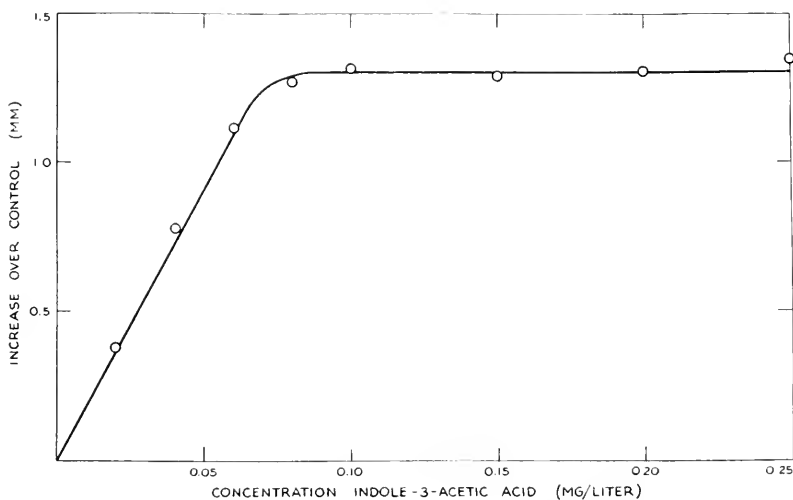


FIG. 1.—Relation between concentration of applied growth substance and straight growth.

root medium provides firm anchorage for the seedlings which facilitates the operations of decapitation, removal of the leaf, and application of the block. The use of test tubes greatly expedites the removal and rearrangement of the plants in the racks in preparing uniform sets. The large test blocks are more easily applied and make better contact when applied terminally. No handling of the seedlings is necessary between the time of initial planting and of testing.

These practical advantages, as well as some others, apply also to the use of agar in test tubes for the growth of seedlings to be used in the curvature test. The seeds may be planted very close to the top of the tubes so that practically none of the coleoptile is obscured in photographing. The tubes allow the plant to be revolved about its long axis

so that the plane of curvature can be placed parallel to that of the photographic paper. Deseeding may be very easily accomplished with a small section lifter or with forceps.

Some disadvantages of the method should be mentioned also. The size of the plants used is a relatively critical factor in comparative studies. It has been found that with the uniform conditions employed the time at which the seedlings will be ready for use can be predicted, at the time of planting, to within 2 or 3 hours. It is essential that this be considered in planning the various operations. The individual variability of the seeds used is such that only about 75 percent of the plants are ready at one time. In a limited series, therefore, there will be considerable waste. In an extended series of tests, involving a few hundred plants, if the larger plants are used first the smaller ones will attain a suitable size by the time they are needed so that more than 90 percent of the planted seeds can be utilized.

SUMMARY

An assay method for growth-promoting substances, which utilizes straight growth of the *Avena* coleoptile, is described. The method appears to possess a number of theoretical and practical advantages over the widely used curvature test.

LITERATURE CITED

- AVERY, G. S., JR., BURKHOLDER, P. R., and CREIGHTON, H. B.
 1937. *Avena* coleoptile curvature in relation to different concentrations of certain synthetic substances. Amer. Journ. Bot., vol. 24, no. 4, pp. 226-232.
 BOYSEN-JENSEN, P.
 1936. Growth hormones in plants. English translation by G. S. Avery, Jr., and P. R. Burkholder. McGraw-Hill Book Co.
 DUBUY, H. G.
 1938. A method for extracting growth substances from pigmented tissues. Journ. Agr. Res., vol. 56, no. 2, pp. 155-158.
 SCHNEIDER, C. L., and WENT, F. W.
 1938. A photokymograph for the analysis of the *Avena* test. Bot. Gaz., vol. 99, no. 3, pp. 470-496.
 THIMANN, K. V., and BONNER, J.
 1932. Studies on the growth hormone of plants. II. The entry of growth substance into the plant. Proc. Nat. Acad. Sci., vol. 18, pp. 692-701.
 1933. The mechanism of the action of the growth substance of plants. Proc. Roy. Soc., ser. B, vol. 113, pp. 126-149.
 THIMANN, K. V., and SCHNEIDER, C. L.
 1938. The rôle of salts, hydrogen-ion concentration, and agar in the response of the *Avena* coleoptile to auxins. Amer. Journ. Bot., vol. 25, no. 4, pp. 270-280.

VAN DER WEIJ, H. G.

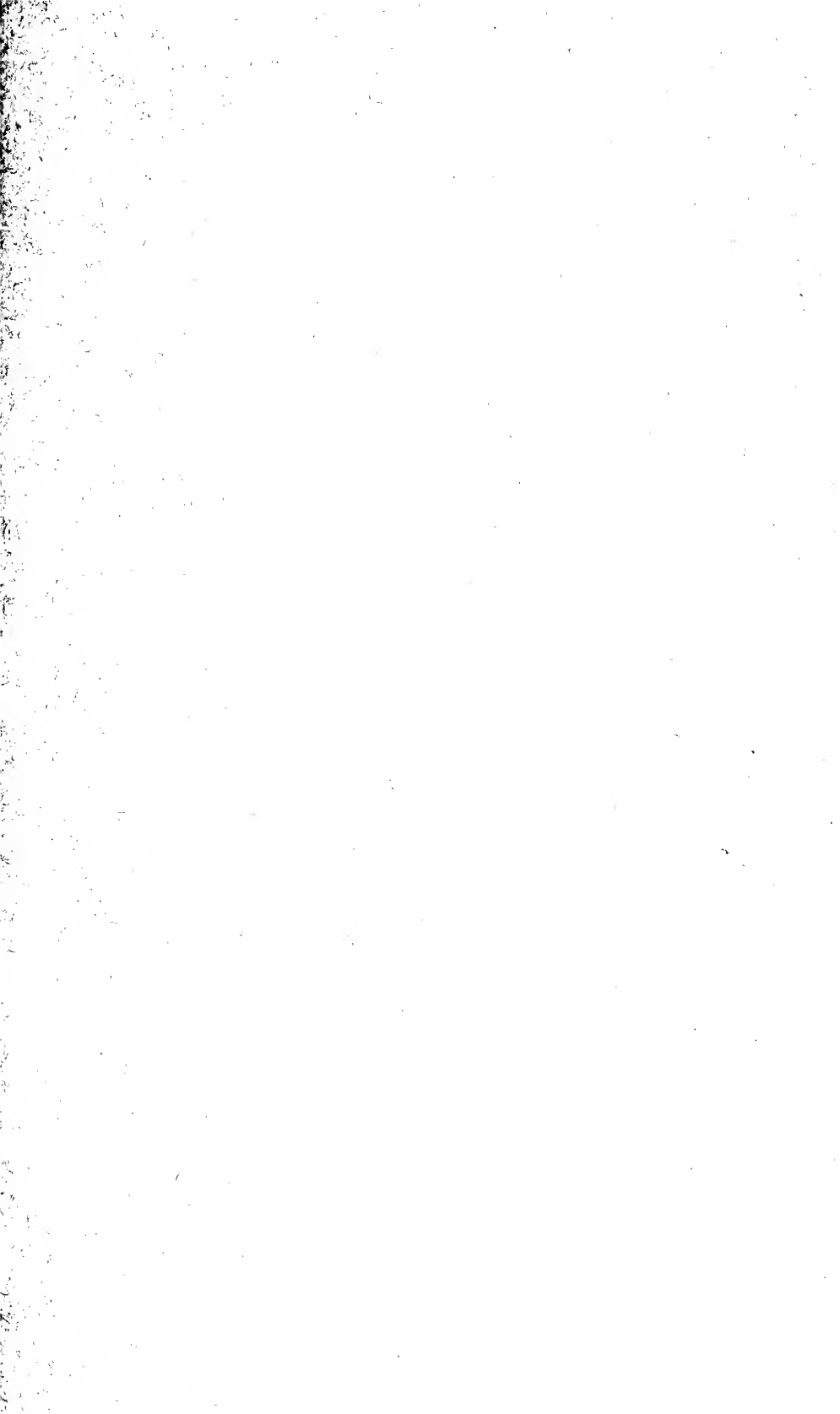
1931. Die quantitative Arbeitsmethode mit Wuchsstoff. Proc. Kon. Akad. Wetensch. Amsterdam, vol. 34, pp. 875-892.

WENT, F. W.

1928. Wuchsstoff und Wachstum. Rec. Trav. Bot. Neerl., vol. 25, pp. 1-116.
- WENT, F. W., and THIMANN, K. V.
1937. Phytohormones. The MacMillan Co.



SHADOWGRAPHS SHOWING FROM TOP TO BOTTOM: INTACT PLANTS PRIOR TO DECAPITATION. DECAPITATED PLANTS IMMEDIATELY AFTER APPLICATION OF AGAR BLOCKS. PLANTS 4 HOURS AFTER APPLICATION OF BLOCKS CONTAINING GROWTH SUBSTANCE. PLANTS 4 HOURS AFTER APPLICATION OF PLAIN AGAR BLOCKS.



SMITHSONIAN MISCELLANEOUS COLLECTIONS

VOLUME 97, NUMBER 12

(End of Volume)

THE SPENCE SHALE AND ITS FAUNA

(WITH SIX PLATES)

BY

CHARLES ELMER RESSER

Curator, Division of Stratigraphic Paleontology,
U. S. National Museum



(PUBLICATION 3490)

CITY OF WASHINGTON

PUBLISHED BY THE SMITHSONIAN INSTITUTION

JANUARY 20, 1939

The Lord Baltimore Press
BALTIMORE, MD., U. S. A.

THE SPENCE SHALE AND ITS FAUNA

By CHARLES ELMER RESSER

*Curator, Division of Stratigraphic Palaeontology,
U. S. National Museum*

(WITH SIX PLATES)

INTRODUCTION

The Spence shale occurs in the northern Wasatch Mountains, in northeastern Utah and adjacent portions of Idaho. Thus far neither this shale nor its fauna has been found south of Brigham, but it is present in both the Wasatch proper and its eastern prong, the Bear River Range. Fossils are everywhere present, sometimes in great abundance and variety.

In 1896 R. S. Spence sent some very interesting and well-preserved Middle Cambrian fossils to Dr. Charles D. Walcott. Correspondence shows that additional material was sent during the next 10 years. Late in the summer of 1906 Dr. Walcott moved camp from Blacksmith Fork to the eastern slopes of the Bear River Range in the vicinity of the locality discovered by Mr. Spence. A brief description of the sections studied in 1906, together with formational names, was published by Walcott in April 1908 (1908a). In December of the same year (1908b) the sections were republished in more detail, including preliminary faunal lists. Unfortunately, the several sections measured in both divisions of the Wasatch were combined into a composite section, thereby obscuring essential stratigraphic facts.

The Spence shale was defined (Walcott 1908a) as "argillaceous shales" about 30 feet thick with "an extremely abundant and varied lower Middle Cambrian fauna," and in the fuller description (Walcott 1908b) the words "and sandy shale" were added. This thin stratigraphic unit was regarded as a member at the base of the Ute formation. It is not a mappable unit and therefore deserves recognition only for its abundant and striking fauna.

The type locality for the Spence shale is in Spence Gulch, which is situated on the eastern slopes of the Bear River Range, about 5 miles southwest of Liberty and 15 miles west of Montpelier, Idaho. Similar beds, but with few fossils, are recognized to the south near Garden City. On the western slope of the Bear River Range, the

Spence shale fauna occurs in the base of the Ute formation in Blacksmith Fork. Deiss (1938) remeasured this section, which forms the standard for the northern Wasatch region, and concluded that the Spence was not present in Blacksmith Fork. But these studies indicate that Walcott's original assignment was probably correct. In the Wasatch proper Spence shale fossils were obtained from Two Mile Canyon, near the northern terminus of the range, and from a belt of unknown extent several miles north of Brigham.

At the latter locality the fauna is found in more calcareous shales than elsewhere. Usually, the Spence shale is a rather soft argillaceous shale, but the fossils are never completely flattened. It seems that fossiliferous lime nodules occur at most localities; at some places these are small, very hard pyritiferous concretions, and at others they consist of crystalline limestone. Irregular oolitic limestone layers are also evidently developed locally.

Shortly after the large collections were made from Spence Gulch in 1906, illustrations of the more conspicuous elements of the fauna were prepared. The 1912 monograph includes the brachiopods, and from time to time trilobite species were described incidentally in other papers. Even the present paper does not describe every species, but it gives a fairly accurate concept of the fauna, only a few obscure forms remaining. Neither are the large number of embryonic specimens considered.

The strata in the Pend Oreille Lake region (Resser, 1938) are the only precise equivalents of the Spence shale. Close affinities exist southward in the Wasatch and southwestward from and including the Ophir shale of the Oquirrh Range. Exact correlations are not attempted until several other faunas have been studied.

In order to save many repetitions of locality descriptions, they are placed here in full, and reference is made to them in the text by number only.

Locality 55c.—Middle Cambrian, Spence shale; about 5 miles southwest of Liberty, 15 miles west of Montpelier, Bear River Range, Idaho.

Locality 51L.—Middle Cambrian, Spence shale; Blacksmith Fork, about 10 miles east of Hyrum, Bear River Range, Utah.

Locality 55e.—Middle Cambrian, Spence shale; mouth of first small canyon south of Wasatch Canyon, east of Lakeview Ranch, $4\frac{1}{2}$ miles north of Brigham, Wasatch Mountains, Utah.

Locality 20x.—Middle Cambrian, "Langston," Spence, Ute; near top of gulch, about 2 miles north of Brigham City, Wasatch Mountains, Utah.

Locality 5g.—Middle Cambrian, Spence shale; Two Mile Canyon, 2 miles southeast of Malad, Wasatch Mountains, Idaho.

Locality 32x.—Middle Cambrian, Ute, Spence, Bloomington; Wasatch Canyon, 5 miles north of Brigham, Wasatch Mountains, Utah.

It will be observed that part of the collections from all but localities 55c and 54L consists of other than Spence shale fossils. Consequently, assignment of species to the Spence shale is certain only for locality 55c where all fossils came from a thin bed with no chance for admixture, and locality 5g on the western side of the Wasatch Mountains. Species believed to represent the Spence fauna have been chosen from the collections of localities 55e, 20x, and 32x. This choice is based on lithology and generic assemblages on hand pieces of rock.

Westonia ella (Hall and Whitfield) was described originally from locality 55e. At several places this species presumably appears in the Spence shale fauna, but evidently is present also in the higher beds of the Ute formation. However, since the species was not found at Spence Gulch, it has been omitted from the illustrations.

Zacanthoides is present also in localities 55e and 20x, but the species are not identifiable owing to the fragmentary nature of the material.

The Archæocyathinae are possibly represented (pl. 1, fig. 39).

DESCRIPTION OF SPECIES

ALGAE

MORANIA Walcott, 1919

MORANIA, sp. undet.

Plate 1, fig. 40

A few Spence shale surfaces show flat algae of the *Morania* type. *Morania* is found in highly fossiliferous argillaceous shales almost everywhere in Lower and Middle Cambrian strata.

Locality 55c.

Figured specimen.—U.S.N.M. no. 96491.

ECHINODERMATA

EOCRINUS Jaekel, 1918

EOCRINUS LONGIDACTYLUS (Walcott)

Plate 1, figs. 41, 42

Eocystites?? longidactylus WALCOTT, U. S. Geol. Surv. Bull. 30, p. 94, pl. 5, fig. 3; pl. 6, fig. 1, 1886.

Eocrinus longidactylus JAEKEL, Pal. Zeitschr., vol. 3, p. 24, 1918.

The identification of this species is not altogether certain, but as far as the state of preservations allows, careful comparison seems to indicate that it should be so identified.

Localities 55c and 55e.

Cotypes.—U.S.N.M. no. 15315; plesiotypes, no. 96492.

WORMS

SELKIRKIA Walcott, 1911

SELKIRKIA SPENCEI, n. sp.

Plate 1, figs. 34, 35

This species from the Spence shale averages smaller than *S. major*. The rate of taper is also less, so that the margins of *S. spencei* are almost parallel.

Localities 55c, 55e, and 54L.

Cotypes.—U.S.N.M. no. 96493.

BRACHIOPODA

MICROMITRA Meek, 1873

MICROMITRA LEPIDA, n. sp.

Plate 1, figs. 11-13

This species is characterized by its large size, many of the shells measuring 10 mm long and 7 mm wide. The ventral valve is rather highly elevated. The dorsal valve preserves internal markings which are the first to be found in any species of the genus. The surface of both valves is ornamented with the usual strong growth lines, and both valves show fine ribbing.

Locality 55c.

Cotypes.—U.S.N.M. no. 51458.

IPHIDELLA Walcott, 1905

IPHIDELLA GRATA, n. sp.

Plate 1, figs. 14-18

This brachiopod was referred by Walcott to *I. pannula*, but its large size alone distinguishes it from the numerous species referred to *I. pannula*, except certain ones in the Grand Canyon and from localities northward of Montana. The characteristic ornamentation is beautifully developed and covers practically the entire shell with equal intensity. The hinge line is rather long and on the dorsal valve

is nearly straight. The crenulated ornamentation gives way somewhat at the outer margin of old shells to strong growth lines.

Localities 55c and 54L.

Cotypes.—U.S.N.M. nos. 51448, 27444.

LINGULELLA Salter, 1866

LINGULELLA EUCHARIS, n. sp.

Plate 1, figs. 1-3

The *Lingulella* species in the Spence shale was referred to the Upper Cambrian species, *L. desiderata*. *L. eucharis* is of medium size averaging about 3 mm in length. The illustrations show that it averages broader than any of the numerous species referred to *L. desiderata*. Growth lines are normally defined, and the usual faint ribbing shows where the outer surface of the shell is exfoliated.

Localities 55c and 55e.

Cotypes.—U.S.N.M. nos. 51704, 51826.

ACROTHELE Linnarsson, 1876

ACROTHELE AFFINIS, n. sp.

Plate 1, figs. 19-22

The Spence shale species of *Acrothele* was referred to *A. subsidua*, but it averages larger and differs further in the more central position of the apex. The ventral valve had considerable elevation. The exterior of both valves is marked by strong growth lines. Well-preserved outer surfaces show characteristic crenulations. The average size of the shells is about 8 mm.

Localities 55c, 55e, and 20x.

Cotypes.—U.S.N.M. no. 52015.

ACROTRETA Kutorga, 1848

ACROTRETA DEFINITA Walcott

Plate 1, figs. 7-10

Acrotreta definita WALCOTT, Proc. U. S. Nat. Mus., vol. 25, p. 584, 1902; U. S. Geol. Surv. Mon. 51, p. 683, pl. 64, figs. 2, 3, 1912.

Locality 55c.

Holotype and paratypes.—U.S.N.M. no. 35270.

ACROTRETA LEVATA, n. sp.

Plate 1, figs. 4-6

Another species with a very high ventral valve occurs with *A. definita*. Besides the height of the ventral valves, this species is characterized by its strong growth lines and the narrowness of the false pedicle groove.

Locality 55c.

Cotypes.—U.S.N.M. no. 52108.**WIMANELLA Walcott, 1908**

Walcott proposed *Wimanella* for smooth, nonplicate brachiopods. He failed to observe that his specimens of the type species were not well preserved and that the ribs were effaced. Because of this error many species of *Wimanella* have been referred to *Nisusia*. In fact, most Middle Cambrian forms referred to *Nisusia* are *Wimanella*, but thus far the genus does not extend above the Middle Cambrian.

WIMANELLA SPENCEI (Walcott)

Plate 1, figs. 27, 28

Nisusia (Jamesella) spencei WALCOTT, U. S. Geol. Surv. Mon. 51, p. 737, text fig. 62, pl. 93, figs. 7, 7a, 1912.

Localities 55c, 20x, and 32x.

Cotypes.—U.S.N.M. no. 52435; plesiotypes, no. 96498.**WIMANELLA RARA (Walcott)**

Plate 1, fig. 29

Nisusia rara WALCOTT, (part), Smithsonian Misc. Coll., vol. 53, no. 3, p. 97, pl. 9, fig. 13a, 1908; U. S. Geol. Surv. Mon. 51, p. 729, text fig. 60, 1912.

It is possible that this single shell is not a good species but merely a peculiarly preserved specimen of *W. spencei*.

Locality 55c.

Holotype.—U.S.N.M. no. 52295.**WIMANELLA NAUTES (Walcott)**

Plate 1, figs. 23-26

Nisusia (Jamesella) nautes WALCOTT, U. S. Geol. Surv. Mon. 51, p. 734, pl. 93, figs. 6-6b, 1912.

Locality 55c.

Cotypes.—U.S.N.M. no. 52432; plesiotypes, no. 96497.

GASTROPODA

HYOLITHES Eichwald, 1840**HYOLITHES CECROPS** Walcott

Plate 1, figs. 36-38

Hyolithes cecrops WALCOTT, Smithsonian Misc. Coll., vol. 67, no. 2, p. 27, pl. 5, figs. 3-3c, 1917.

Hyolithes idahoensis RESSER, idem, vol. 97, no. 3, p. 5, pl. 1, figs. 57, 58, 1938.

This is an abundant species, but owing to its large size and shale matrix, few complete specimens are available. Numerous operculae are preserved. Assembly of many specimens shows that the Spence shale form, together with that in the Rennie shale, is identical with the Ross Lake shale species.

Ross Lake; (loc. 63j) Popes Peak, $1\frac{1}{2}$ miles south of Stephen, and other localities, British Columbia.

Rennie; (loc. 37m) North Gold Creek, Pend Oreille Lake.

Spence; localities 55c, 55e, and 54L.

Cotypes.—U.S.N.M. no. 63724; plesiotypes, nos. 95021, 96496.

HYOLITHES ORNATELLUS, n. sp.

Plate 1, figs. 30-32

This is the most highly ornamented species of *Hyolithes* known. The anterior side is flat and depressed below the rounded margins, while the posterior surface is arched. Strong striations run at right angles to the axis on the anterior surface, but on the posterior are parallel with the front margin.

Locality 55c.

Cotypes.—U.S.N.M. no. 96494.

"ORTHOTHECA" SOLA, n. sp.

Plate 1, fig. 33

A single conical tube was found among the thousands of Spence shale fossils. This shell has nearly a circular cross-section and is about 8 mm long and 4 mm wide at the aperture.

Locality 55c.

Holotype.—U.S.N.M. no. 96495.

AGNOSTIDA

AGNOSTUS Brongniart, 1822**AGNOSTUS BONNERENSIS** Resser

Plate 2, figs. 24-26

Agnostus bonnerensis RESSER, Smithsonian Misc. Coll., vol. 97, no. 3, p. 6, pl. 1, figs. 16, 17, 1938.

This species is abundant in the Spence shale.

Middle Cambrian, Lakeview; (loc. 37n) Lakeview, Pend Oreille Lake, Idaho.

Locality 55c.

Plesiotypes.—U.S.N.M. no. 96499.

AGNOSTUS BRIGHAMENSIS, n. sp.

Plate 2, figs. 27-29

Photographs of this species are mounted to show the associated fauna, *Oryctocephalus*, *Pagetia*, *Clavaspidello*, and *Lingulella*.

Compared with *A. bonnerensis*, this species differs first in its more circular outline for both shields. Little further difference is noticeable in the head. A sharp difference is brought about in the pygidium by the deeper transverse rhachial furrows but more particularly by the failure of the rear rhachis to penetrate the pleural lobe.

Locality 20x.

Holotype and paratypes.—U.S.N.M. no. 96500.

TRILOBITA

PAGETIDAE Kobayashi

PAGETIA Walcott, 1916**PAGETIA CLYTIA** Walcott

Plate 2, figs. 30-32

Pagetia clytia WALCOTT, Smithsonian Misc. Coll., vol. 64, no. 5, p. 408, pl. 67, figs. 2-2c, 1916.

In spite of the great abundance of this trilobite it is difficult to find really good specimens.

Localities 55c and 20x.

Cotypes.—U.S.N.M. nos. 62862-7.

ZACANTHOIDEA Swinnerton

ZACANTHOIDES Walcott, 1888

ZACANTHOIDES IDAHOENSIS Walcott

Plate 3, figs. 18-20

Zacanthoides idahoensis WALCOTT (part), Smithsonian Misc. Coll., vol. 53, no. 2, p. 26, pl. 3, figs. 1, 6, 1908. [Not figs. 2-5, 10 = *Z. holopygus*; figs. 7 = *Z. disjunctus*; figs. 8, 9, 11 = *Z. gradatus*.]

This species is now restricted by elimination of three other species included among the original illustrations. Walcott mentioned the different forms present but did not carry his observations to their logical conclusion.

Locality 55c.

Lectotype.—U.S.N.M. no. 53434; paratypes, nos. 53432, 53438.

ZACANTHOIDES ADJUNCTUS, n. sp.

Plate 3, figs. 13, 14

Zacanthoides idahoensis WALCOTT (part), Smithsonian Misc. Coll., vol. 53, no. 2, p. 26, pl. 3, fig. 7, 1908. (See *Z. idahoensis*.)

Walcott figured a pygidium of this species. The pygidium of *Z. adjunctus* is characterized by a wide axis and extensive fusion of the pleura, so that the tail makes a far more solid plate than in *Z. idahoensis*. The outer spine is long but is free only as far as the end of the axis. The second pair of spines is fairly long, but slender, and the remaining three pairs of spines are short and sharp-pointed.

Locality 55c.

Holotype and paratypes.—U.S.N.M. nos. 53429, 53427.

ZACANTHOIDES GRADATUS, n. sp.

Plate 3, figs. 15-17

Zacanthoides idahoensis WALCOTT (part), Smithsonian Misc. Coll., vol. 53, no. 2, p. 26, pl. 3, figs. 8, 9, 11, 1908. (See *Z. idahoensis*.)

This species is characterized by a rather broad pygidial axis. The marginal spines decrease in size slightly for the first three pairs; then abruptly for the remainder. It is thus that the species is distinguished chiefly from *Z. idahoensis* in which the pygidial spines continue to decrease at a fairly even rate from the outer to the inner pair.

The cranium is referred to the species on the basis of its wide glabella.

Locality 55c.

Holotype.—U.S.N.M. no. 96521; paratypes, nos. 53430-1, 3.

ZACANTHOIDES ABBREVIATUS, n. sp.

Plate 2, figs. 7-9

Z. abbreviatus is represented by fewer specimens than most other species in the Spence shale. It is characterized by a rather wide axis and a considerable degree of fusion in the pygidium. Like *Z. idahoensis* the pygidial spines decrease in size at a regular rate from the outer to the inner pair. But these spines are shorter, the axis stouter and the degree of fusion of the pygidium greater than in *Z. idahoensis*.

Locality 55c.

Holotype and paratypes.—U.S.N.M. no. 96501.**ZACANTHOIDES SERRATUS, n. sp.**

Plate 2, figs. 4-6

This small species is relatively uncommon. Walcott had illustrations of this distinctive pygidium prepared, but recognizing it as a separate species, did not publish the figures. Aside from the slender axis throughout, the rather long thoracic pleura and the pygidial structure characterize the species. In it the spines are fused but remain distinct, terminating in rather broad short spines. These spines terminate at nearly a straight line, hence give the rear of the pygidium its serrate margin.

Locality 55c.

Holotype and paratypes.—U.S.N.M. no. 96502.**ZACANTHOIDES HOLOPYGUS, n. sp.**

Plate 2, figs. 10-12

Zacanthoides idahoensis WALCOTT (part), Smithsonian Misc. Coll., vol. 53, no. 2, p. 26, pl. 3, figs. 2-5, 10, 1908. (See *Z. idahoensis*.)

At first it was thought that this small species was merely a young stage of one of the larger forms, but careful sorting shows that such is not the case. *Z. holopygus* varies in length from less than one-eighth of an inch to more than 2 inches. As a whole this trilobite has a more even oval shape than most species of *Zacanthoides*, which is due to the fact that the thoracic terminations are relatively broader. It is the most common Spence shale species.

Z. holopygus has rather large eyes, and the anterior facial suture diverges sharply, leaving rather long anterior angles. The pygidium is fused into a solid shield, including all marginal spines except the

outer pair, the other spines being reduced to a serrated border. The long thoracic spine is not on the fifth but the last segment.

Locality 55c.

Holotype.—U.S.N.M. no. 96522; paratypes, nos. 53435-6-7, 53440.

DOLICHOMETOPINAE Walcott

BATHYURISCUS Meek, 1873

BATHYURISCUS ATOSSA Walcott

Plate 5, fig. 15

Bathyriscus atossa WALCOTT, Smithsonian Misc. Coll., vol. 64, no. 5, p. 336, pl. 48, figs. 2, 2a-b, 1916. RESSER, Smithsonian Misc. Coll., vol. 93, no. 5, p. 15, 1935.

Locality 55c.

Lectotype.—U.S.N.M. no. 62642; paratypes, nos. 62643-4.

BATHYURISCUS BRIGHAMENSIS, n. sp.

Plate 5, figs. 3, 4

This species is fully typical of the genus. It is characterized by a rather wide glabella, nine thoracic segments, and a rather wide pygidium. A broad indentation notches the rear margin rather deeply, and the anterior marginal pygidial spines are small.

The holotype evidently is a pathological specimen, for the anterior pleural segments on the right side have coalesced and in healing an injury have produced an extraordinarily long spine.

Locality 20x.

Holotype and paratype.—U.S.N.M. no. 96524.

POLIELLA Walcott, 1916

POLIELLA CARANUS (Walcott)

Plate 2, fig. 21

Bathyriscus (Poliella) caranus WALCOTT, Smithsonian Misc. Coll., vol. 64, no. 5, p. 350, pl. 46, fig. 5, 1916.

Poliella caranus RESSER, Smithsonian Misc. Coll., vol. 93, no. 5, p. 44, 1935.

Locality 55c.

Holotype.—U.S.N.M. no. 62628.

POLIELLA ANTEROS Walcott

Plate 2, figs. 19, 20

Bathyriscus (Poliella) anteros WALCOTT, Smithsonian Misc. Coll., vol. 64, no. 5, p. 349, pl. 46, fig. 5, 1916.

Locality 55c.

Holotype.—U.S.N.M. no. 62622.**GLOSSOPLEURA** Poulsen, 1927**GLOSSOPLEURA BION** (Walcott)

Plate 5, figs. 1, 2

Dolichometopus bion WALCOTT, Smithsonian Misc. Coll., vol. 64, no. 5, p. 363, pl. 52, figs. 2-2c, 1916.

Glossopleura bion RESSER, Smithsonian Misc. Coll., vol. 93, no. 5, p. 32, 1935.

Locality 55c.

Cotypes.—U.S.N.M. nos. 62709-12.**GLOSSOPLEURA SIMILARIS**, n. sp.

Plate 5, figs. 9-11

This species is similar to *G. producta*. The eyes, however, are shorter and the palpebral lobes smaller, and in the pygidium fusion is less complete. The species is characterized by a rather narrow pygidial border, a narrow doublure, and segmentation in both axis and pleural lobes. The palpebral lobes are strongly bowed. Fine irregular lines cover the surface.

Localities 55c and 54L.

Holotype.—U.S.N.M. no. 96525; paratypes, no. 96526.**GLOSSOPLEURA UTAHENSIS** Resser

Plate 5, fig. 16

Bathyriscus productus WALCOTT (part), U. S. Geol. Surv. Bull. 30, p. 217, pl. 30, figs. 1, 1b, 1886.

Bathyriscus anax WALCOTT (part), Smithsonian Misc. Coll., vol. 64, no. 5, p. 335, pl. 48, fig. 1b, 1916.

Glossopleura utahensis RESSER, Smithsonian Misc. Coll., vol. 93, no. 5, p. 33, 1935.

The pygidium, identified with *Clavaspidella anax*, is refigured.

Locality 55e. (Holotype locality 30a, Big Cottonwood Canyon, Wasatch Mountains.)

Holotype and paratypes.—U.S.N.M. nos. 62641, 62639.

GLOSSOPLEURA GIGANTEA, n. sp.

Plate 5, fig. 17

This is the largest species known in the genus, and is moreover one of the largest Middle Cambrian trilobites known except, of course, the enormous species of *Paradoxides*. The holotype is over 5 inches long, and other fragments show that the average size is nearly as great.

This species is characterized by a large glabella, somewhat swollen in front. There appear to be 8 thoracic segments. Compared with other Middle Cambrian species, the pygidium of *G. gigantea* has a distinctly circular outline.

Locality 20x.

Holotype.—U.S.N.M. no. 96527.**CLAVASPIDELLA Poulsen, 1927****CLAVASPIDELLA BITHUS (Walcott)**

Plate 5, fig. 12

Bathyuriscus? bithus WALCOTT, Smithsonian Misc. Coll., vol. 64, no. 5, p. 340, pl. 47, figs. 4, 4a, 1916.

Clavaspidella bithus RESSER, Smithsonian Misc. Coll., vol. 93, no. 5, p. 20, 1935.

Locality 55c.

Lectotype.—U.S.N.M. no. 62635; paratype, no. 62636.**CLAVASPIDELLA ANAX (Walcott)**

Plate 5, figs. 5, 6

Bathyuriscus anax WALCOTT (part), Smithsonian Misc. Coll., vol. 64, no. 5, p. 335, pl. 48, figs. 1, 1a, c, d, 1916.

Clavaspidella anax RESSER, Smithsonian Misc. Coll., vol. 93, no. 5, p. 21, 1935.

Localities 55e and 32x.

Lectotype.—U.S.N.M. no. 62637; paratypes, nos. 62638-40.**ORYCTOCEPHALIDAE Raymond****ORYCTOCEPHALUS Walcott, 1886****ORYCTOCEPHALUS WALCOTTI Resser**

Plate 2, figs. 15-18

Oryctocephalus walcotti RESSER (part), Smithsonian Misc. Coll., vol. 97, no. 3, p. 9, pl. 1, fig. 23, 1938.

This species is common in the Spence shale.

Middle Cambrian, Lakeview; near Lakeview, Pend Oreille Lake, Idaho.

Localities 55c and 5g.

Plesiotypes.—U.S.N.M. nos. 96503-4.

ORYCTOCARE Walcott, 1908

ORYCTOCARE GEIKEI Walcott

Plate 2, figs. 22, 23

Oryctocare geikei WALCOTT, Smithsonian Misc. Coll., vol. 53, no. 2, p. 23, pl. 1, figs. 9, 10, 1908.

No additional specimens of this rare trilobite were found when the thousands of specimens from the locality were again examined. The mistaken reference of this species to *Oryctocephalus* and *Utia* in the Lakeview limestone of Pend Oreille Lake, Idaho, has been adjusted elsewhere.

Locality 55c. Lakeview; near Lakeview, Pend Oreille Lake, Idaho.

Lectotype and paratypes.—U.S.N.M. nos. 53426-28.

LEIOSTEGIDAE Bradley

OLENOIDES Meek, 1877

OLENOIDES WAHSATCHENSIS (Hall and Whitfield)

Plate 4, figs. 1, 2

Dikellocephalus wahsatchensis HALL and WHITFIELD, U. S. Geol. Expl. 40th Par., vol. 4, p. 241, pl. 1, fig. 35, 1877.

Dikellocephalus ? gothicus HALL and WHITFIELD, U. S. Geol. Expl. 40th Par., vol. 4, p. 242, pl. 1, fig. 36, 1877.

Olenoides wahsatchensis WALCOTT, U. S. Geol. Surv. Bull. 39, p. 189, pl. 29, figs. 2, 2a, 1886.

Locality 20x.

Cotypes.—U.S.N.M. no. 15447.

OLENOIDES BRIGHAMENSIS, n. sp.

Plate 3, figs. 8, 9

This is a small species associated with *Ehmaniella* and differs from the other two Wasatch species in several respects. The cranidium does not depart from the norm, and is rather highly arched in both directions. The pygidium has six pairs of marginal spines which are rather short.

Locality 20x.

Holotype and paratype.—U.S.N.M. no. 96513.

OLENOIDES EVANSI, n. sp.

Plate 4, figs. 3, 4

This species is characterized by a quadrate glabella similar to species of *Kootenia*, but the pygidium has the true *Olenoides* feature of separate pleura. It has seven pairs of spines. The pygidium of *O. evansi* resembles that of *O. clongatus* due to its triangular shape and elongation to accommodate seven spines. The occipital ring and thoracic segments each bear a small median spine or tubercle, which are lacking from the axial rings of the pygidium.

A crushed and poorly preserved hypostoma occurs with portions of a few pygidia and is thought to belong to the species.

Locality 55e.

Holotype and paratype.—U.S.N.M. no. 96514.

KOOTENIA Walcott, 1888**KOOTENIA IDAHOENSIS, n. sp.**

Plate 3, figs. 1-3

This species belongs to the *serrata* group of the genus and is a six-spined form. The cranidium has the usual quadrate outline and proportions, and the surface is ornamented with lines and granules. The neck spine is slender and not very long.

The thorax has seven segments terminating in rather blunt spines, which have the usual elongate, scaly granulations.

Six blunt spines margin the pygidium. All spines are coarsely granulated.

Locality 55c.

Holotype and paratypes.—U.S.N.M. no. 96505.

KOOTENIA SPENCEI, n. sp.

Plate 3, figs. 4, 5

Only two incomplete pygidia have been found of this seven-spined species. Unfortunately, neither pygidium is well preserved. The pleural grooves remain on exfoliated specimens. Six pairs of the marginal spines are long and slender, possibly attaining a length greater than the pygidium. Each spine had a medial furrow for a considerable distance from the border. The seventh pair of spines is short.

Locality 55c.

Holotype and paratypes.—U.S.N.M. no. 96506.

KOOTENIA MATHEWSI, n. sp.

Plate 3, figs. 6, 7

This species belongs to the seven-spined group. It is characterized by long, round spines, the longest likely exceeding the length of the pygidium. The seventh pair is short and slender.

This species is very similar to *K. spencei*, being distinguished by the smaller spread and curvature of the spines and their lack of median grooves.

Locality 20x.

Holotype and paratype.—U.S.N.M. no. 96507.**KOOTENIA GRACILIS, n. sp.**

Plate 3, figs. 11, 12

This beautiful trilobite is associated with *Ehmaniella* and *Olenoides brighamensis* in the thin limestone layers intercalated in the shales.

K. gracilis is one of the few six-spined species in the genus. Evidently the seventh pair, which is usually greatly reduced, has become altogether obsolescent. The glabella is long, but otherwise the cranium is normal in all respects. Fusion is normal in the pygidium and the long, slender spines are straight and hence well spread out.

Locality 20x.

Holotype and paratype.—U.S.N.M. no. 96508.

PTYCHOPARIDAE Matthew

ALOKISTOCARE Lorenz, 1906**ALOKISTOCARE IDAHOENSE, n. sp.**

Plate 4, figs. 8, 9

This species has 23 or 24 thoracic segments and is finely granulated on the outer surface. Exfoliated surfaces show lines and punctation. The genal spines extend back to about the fifth thoracic segment. The pygidium is completely fused.

Locality 55c.

Holotype and paratype.—U.S.N.M. no. 96507.**ALOKISTOCARE SPENCENSE, n. sp.**

Plate 4, figs. 10, 11

This is also an abundant species associated with *A. idahoense*. Compared to that species, *A. spencense* is characterized by a narrower

cranidium. In keeping with that narrowness, the trilobite as a whole is more slender.

Localities 55c, 55e, and 20x.

Holotype and paratypes.—U.S.N.M. no. 96516.

ALOKISTOCARE LATICAUDUM, n. sp.

Plate 4, figs. 15-19

This species is characterized by a wide brim and wide, long, genal spines, a wide pygidium and 17 thoracic segments. The genal spines extend back to about the 14th segment. Fusion has not obliterated pleural furrows in the pygidium.

Localities 55c and 55e.

Holotype and paratype.—U.S.N.M. nos. 96517, 8.

ALOKISTOCARE SEPTUM, n. sp.

Plate 4, figs. 5-7

This is a wide-tailed form like *A. laticaudum*. It differs in having a narrower glabella. But the distinctive feature is the great genal spines which extend almost to the pygidium.

Locality 55c.

Holotype and paratype.—U.S.N.M. no. 96520.

ALOKISTOCARE PUNCTATUM, n. sp.

Plate 4, figs. 20, 21

Reduction of brim brings this species closer to *Chancia*, than most species referred to *Alokistocare*. But since a rim is not differentiated by thickening, this form is called *Alokistocare*.

The cranidium is rather wide and the anterior margin not so much curved. On exfoliated specimens the eye lines are heavy and the surface is strongly punctate. One specimen retains 15 thoracic segments, indicating a thorax of possibly 20 segments.

Locality 55e.

Holotype and paratypes.—U.S.N.M. no. 96519.

CHANCIA Walcott, 1924

CHANCIA EBDOME Walcott

Plate 4, figs. 12-14

Chancia ebdome WALCOTT, Smithsonian Misc. Coll., vol. 75, no. 2, p. 55, pl. 10, fig. 4, 1924. Idem, no. 3, p. 80, pl. 17, fig. 26, 1925.

Locality 55c.

Holotype.—U.S.N.M. no. 70274.

CHANCIA EVAX Walcott

Plate 5, figs. 18, 19

Chancia evax WALCOTT, Smithsonian Misc. Coll., vol. 75, no. 3, p. 81, pl. 17, fig. 27, 1925.

Localities 55c and 55e.

Holotype.—U.S.N.M. no. 70275.**CHANCIA ANGUSTA**, n. sp.

Plate 5, figs. 13, 14

This species differs from *C. abdome* chiefly in that the cranium is narrower, and that the surface of the head is more finely granulose. *C. angusta* is characterized by a glabella which tapers at the usual rate and attains slightly more than half the cranial length. Three pairs of furrows are faintly defined, the rear pair being directed sharply backward. Eyelines are well developed on the under side of test. Eyes moderately elevated.

Exfoliated specimens have all furrows accentuated, and the double impression modifies the appearance of the unfurrowed brim.

Locality 55c.

Holotype and paratypes.—U.S.N.M. no. 96523.**ALOKISTOCARELLA** Resser, 1938**ALOKISTOCARELLA SPENCEI**, n. sp.

Plate 3, fig. 10

This species is represented by several cranidia, all of which are, unfortunately, almost entirely exfoliated. This, of course, accentuates all furrows and ridges. *A. spencei* is characterized by a truncate glabella of normal size and an upturned narrow rim. The width of the fixigene at the eye is about equal to that of the glabella at the same point, which makes the cranium wide.

Locality 55c.

Holotype.—U.S.N.M. no. 96509.**ELRATHIA** Walcott, 1924**ELRATHIA SPENCEI**, n. sp.

Plate 6, figs. 15-17

This species has 17 thoracic segments. The cranium is wide, the glabella occupying about three-fourths its length. The small pygidium is characteristic of the genus, and it has an indented rear margin.

Locality 55c.

Holotype and paratypes.—U.S.N.M. no. 96540.

ELRATHIA RARA, n. sp.

Plate 6, fig. 18

This species is based on a single individual, consisting of the cranidium and 17 segments. Most of the cranidium is exfoliated, and shows strong striations on the preglabellar area. A narrow, straight rim is demarcated.

Locality 55c.

Holotype.—U.S.N.M. no. 96541.**ELRATHINA Resser, 1937****ELRATHINA OFFULA, n. sp.**

Plate 2, figs. 13, 14

This genus and species is represented by only a few cranidia. The illustrations show the relative proportion of the several parts, the characteristic constriction of brim width, and the slightly concave brim, with the rim only weakly defined. Eyes are rather small.

Locality 55c.

Holotype and paratype.—U.S.N.M. no. 96510.**EHMANIELLA Resser, 1937****EHMANIELLA QUADRANS (Hall and Whitfield)**

Plate 6, figs. 28-32

Crepicephalus? (*Loganellus*) *quadrans* HALL and WHITFIELD, U. S. Geol. Expl. 40th Par., vol. 4, p. 238, pl. 2, figs. 11-13, 1877.

Ptychoparia quadrans WALCOTT, U. S. Geol. Surv. Bull. 30, p. 199, pl. 29, figs. 4, 4a, b, 1886; Smithsonian Misc. Coll., vol. 64, p. 204, 1916.

Ehmaniella quadrans RESSER, Smithsonian Misc. Coll., vol. 95, no. 22, p. 10, 1937.

Localities 20x, 55e, and 54L.

Holotype and paratypes.—U.S.N.M. no. 15432; plesiotype, no. 96539.

CLAPPASPIS Deiss, 1939

The genotype, *C. typica* Deiss, comes from the Pentagon shale of Lewis and Clark Range, Montana. Average size and shape, normal development of eye lines and furrows, and eyes situated slightly behind the middle of the head, characterize the genus. All species are evidently ornamented by some sort of granulated surface. Deiss did not have any entire individuals and so could not illustrate the thorax. Several Spence shale individuals have 14 thoracic segments.

Five species in the Spence shale are referred to *Clappaspis*.

Clappaspis appears to be related to *Ehmaniella* or at least most closely resembles that genus. The only differences of consequence are the slightly narrower preglabellar area and the granulated surface, for the pygidia are clearly constructed on the same plan.

CLAPPASPIS SPENCEI, n. sp.

Plate 6, figs. 5, 6

This is the widest of the five species recognized in the Spence shale. It is further distinguished by two sets of granules rather evenly distributed, the smaller ones being more numerous. Exfoliated specimens have coarse irregular striations on the preglabellar area.

Locality 55c.

Holotype and paratypes.—U.S.N.M. no. 96530.

CLAPPASPIS IDAHOENSIS, n. sp.

Plate 6, figs. 26, 27

Three complete individuals represent this species. The cranium is narrower than *C. spencei* and has a shorter, more conical glabella. *C. idahoensis* is characterized by scattered granules of uneven size. The thorax has 14 segments.

Locality 55c.

Holotype and paratypes.—U.S.N.M. no. 96531.

CLAPPASPIS LANATA, n. sp.

Plate 6, fig. 7

A single cranium represents this species, which has a narrow cranium, long glabella, and the surface is closely crowded with small granules. Rather heavy striations occur on the preglabellar area.

Locality 55c.

Holotype.—U.S.N.M. no. 96532.

CLAPPASPIS CORIACEA, n. sp.

Plate 6, figs. 11, 12

This species is rather wide. Coarse granules are widely scattered over the surface, which is covered with a small set of closely crowded granulations. Exfoliated specimens appear pitted.

Locality 55c.

Holotype and paratypes.—U.S.N.M. no. 96533.

CLAPPASPIS DOTIS, n. sp.

Plate 6, figs. 13, 14

This species is represented by the largest number of specimens. It is characterized by a short glabella, and closely crowded granulations which are of medium size.

Locality 55c.

Holotype and paratypes.—U.S.N.M. no. 96534.

FAMILY UNDESIGNATED

VISTOIA Walcott, 1925**VISTOIA? MINUTA, n. sp.**

Plate 2, figs. 1, 2

One of the illustrated specimens of this species is mounted as a cranidium, but this may be only an accidental resemblance. Certainly most of the examples available are pygidia. Whenever such trilobites as these retain their full relief, difficulty is experienced in distinguishing heads and tails. Consequently, the question is not brought to a final conclusion.

Even though this trilobite is very small, it is referred to *Vistoia* chiefly because it fits no other Middle Cambrian genus in any respect. It may well be that entire specimens will show that the cranidium disagrees with that of *Vistoia prisca* and then a new genus can be erected.

Aside from its small size, *V. ? minuta* is characterized by simplicity. The pygidium has a simple, highly arched semicircular outline. An axis about a third the width of the pygidium is faintly outlined by shallow dorsal furrows, which do not unite in the rear except by the faintest trace. One specimen retains several simple thoracic segments.

Localities 55c and 5g.

Holotype and paratypes.—U.S.N.M. no. 96511.

UTIA Walcott, 1925**UTIA CURIO Walcott**

Plate 2, figure 3

Utia curio WALCOTT, Smithsonian Misc. Coll., vol. 75, no. 2, p. 60, pl. 14, fig. 4, 1924. Idem, no. 3, p. 119, pl. 15, figs. 11-14, 1925. RESSER (part), idem, vol. 97, no. 3, p. 9, pl. 1, figs. 19, 20, 1938.

Several hundred specimens of this unique trilobite have now been segregated. One of the cotype cranidia has about nine thoracic segments attached, but no pygidium has been assigned to the species.

Locality 55c. Lakeview; (loc. 37n) Lakeview, Pend Oreille Lake, Idaho.

Cotypes.—U.S.N.M. nos. 70235-7; plesiotypes, no. 95041.

BYTHICHEILUS, n. gen.

Trilobites of less than average size. Cranidium rather large. Glabella well defined except in front where the dorsal furrow coalesces with the depression in the brim. Fixigenes about as wide as the glabella. Eyelines formed by abrupt depression of anterior fixigenes. Eyes rather large, situated back of the cranidial midpoint. Brim less than one-third cranidial length. Narrow, striated upturned rim clearly defined. Preglabellar area depressed in a peculiar manner, which suggests generic name. Libragenes narrow with moderate genal spines. Striated rim sharply upturned almost to the tip of the genal spines.

Thorax with 14 segments, rather straight, parallel to each other, divided evenly by pleural furrows and bent down rather abruptly at geniculation.

Pygidium small, completely fused, with dorsal furrow shallow and not clearly defined around the rear.

Genotype.—*B. typicum*, new species.

BYTHICHEILUS TYPICUM, n. sp.

Plate 6, figs. 1-4

The generic description and illustrations present the specific features adequately.

Locality 55c.

Holotype and paratypes.—U.S.N.M. no. 96537.

BYTHICHEILUS ALVEATUM, n. sp.

Plate 6, figs. 8-10

This species differs from *B. typicum* in having a longer depression in the preglabellar area, a less upturned rim, less indentation of the front of the glabella by the median depression, and stronger eyeridges due to the more abrupt slope of the brim.

B. alveatum is characterized by a curved anterior margin, fixigenes about three-fourths as wide as the glabella, and by a depressed preglabellar area. Exfoliated specimens show pronounced glabellar furrows and strong eyelines.

Locality 55c.

Holotype and paratypes.—U.S.N.M. no. 96538.

SPENCIA, n. gen.

Small trilobites characterized by a rather large, slightly tapered glabella which extends to the anterior furrow. Brim reduced to thickened rim, wider in the middle than at the ends. This causes the anterior furrow to join the dorsal furrow in front of the glabella. Fixigenes convex, anteriorly nearly as wide as the glabella. Eyelines fairly prominent. Eyes small, situated slightly behind the middle of the head.

Libragenes small, with short but sharp-pointed genal spines.

Thorax has 16 segments. The pygidium is small, trilobate, and well fused.

Surface of cranium and ridges of the thoracic segments marked by scattered granules.

Genotype.—*S. typicalis*, new species.

SPENCIA TYPICALIS, n. sp.

Plate 6, figs. 22-25

This species is characterized by scattered granules and a rather wide space where the anterior and dorsal furrows join.

Locality 55c.

Holotype and paratypes.—U.S.N.M. no. 96535.

SPENCIA PLENA, n. sp.

Plate 6, figs. 19-21

This species is characterized chiefly by the swollen rim and the narrowing of the preglabellar area or rather the anterior and dorsal furrows. Scattered granules occur on the more elevated portions of the cranium.

Locality 55c.

Holotype and paratypes.—U.S.N.M. no. 96536.

STAUROHOLCUS, n. gen.

Small trilobites; only cranidia known. Glabella about three-fourths the length of cephalon, without furrows, truncate with rounded anterior corners, tapering only slightly. Fixigenes fully as wide as glabella. Eyelines faint, but clearly defined. Eyes small, situated about the mid-point. Occipital spine present. Brim rounded at anterior corners. Rim thickened in center, upturned. Preglabellar area

depressed in center, giving rise to the appearance of the anterior and dorsal furrows crossing each other in the center.

Name.—*σταυρος* = cross; *ὄλκος* = furrow.

Genotype.—*S. typicalis*, new species.

STAUROHOLCUS TYPICALIS, n. sp.

Plate 5, figs. 7, 8

The illustrations and generic description portray the specific characters.

Locality 55c.

Holotype and paratypes.—U.S.N.M. no. 96528.

REFERENCES

DEISS, CHARLES.

1938. Cambrian formations and sections in part of Cordilleran trough. Bull. Geol. Soc. Amer., vol. 49, pp. 1067-1168.

1939. Cambrian stratigraphy and trilobites of northwestern Montana. Geol. Soc. Amer., Spec. Paper 18.

RESSER, C. E.

1938. Middle Cambrian fossils from Pend Oreille Lake, Idaho. Smithsonian Misc. Coll., vol. 97, no. 3.

WALCOTT, C. D.

1908a. Nomenclature of some Cambrian Cordilleran formations. Smithsonian Misc. Coll., vol. 53, no. 1, April.

1908b. Cambrian sections of the Cordilleran area, Smithsonian Misc. Coll., vol. 53, no. 5, December.

EXPLANATION OF PLATES

All figures are natural size unless otherwise designated. Species without locality references are all from locality 55c.

PLATE I

	PAGE
<i>Lingulella eucharis</i> , new species.....	5
FIG. 1. Ventral valve ($\times 3$).	
FIGS. 2, 3. Two dorsal valves ($\times 3.5$).	
<i>Acrotreta levata</i> , new species.....	6
FIG. 4. Narrow false pedicle groove ($\times 6$).	
FIG. 5. Interior of ventral valve ($\times 6$).	
FIG. 6. Interior of dorsal valve ($\times 3$).	
<i>Acrotreta definita</i> Walcott.....	5
FIG. 7. Exterior ventral valve ($\times 4$).	
FIGS. 8, 9. Exterior and interior of dorsal valves ($\times 4$).	
FIG. 10. Interior ventral valve ($\times 4$).	
<i>Micromitra lepida</i> , new species.....	4
FIG. 11. Somewhat crushed ventral valve ($\times 1.5$).	
FIGS. 12, 13. Exterior and interior of dorsal valve ($\times 1.5$).	

	PAGE
<i>Iphidella grata</i> , new species.....	4
FIGS. 14, 18. Ventral valves ($\times 3$).	
FIGS. 15, 17. Molds of the exterior surface of dorsal valves ($\times 2$).	
FIG. 16. Dorsal valve ($\times 3$).	
<i>Acrotheca affinis</i> , new species.....	5
FIG. 19. Ventral valve ($\times 2$).	
FIG. 20. Dorsal valve ($\times 1.5$).	
FIGS. 21, 22. Interiors ($\times 2.5$).	
<i>Wimanelia nautes</i> (Walcott).....	6
FIG. 23. Ventral valve ($\times 2$).	
FIG. 24. Dorsal valve ($\times 2$).	
FIG. 25. Dorsal valve ($\times 3$).	
FIG. 26. Ventral valve ($\times 1.5$).	
<i>Wimanelia spencei</i> (Walcott).....	6
FIGS. 27, 28. Ventral valve and mold of exterior.	
<i>Wimanelia rara</i> (Walcott).....	6
FIG. 29. Only specimen known.	
<i>Hyolithes ornatellus</i> , new species.....	7
FIGS. 30, 32. Posterior surface ($\times 2$).	
FIG. 31. Anterior surface ($\times 2$).	
" <i>Orthotheca</i> " <i>sola</i> , new species.....	7
FIG. 33. Round conical tube ($\times 2$).	
<i>Selkirkia spencei</i> , new species.....	4
FIGS. 34, 35. Several flattened tubes.	
<i>Hyolithes cecrops</i> Walcott.....	7
FIG. 36. Posterior surface.	
FIG. 37. Specimen showing cameration.	
FIG. 38. Operculum.	
<i>Archaeocyathus</i> ?	3
FIG. 39. Sides of tubes shown in lower and "ends" turned toward observer in upper portion ($\times 6$).	
<i>Morania</i> , sp. undet.....	3
FIG. 40. Irregular ovate pieces of the alga.	
<i>Eocrinus longidactylus</i> (Walcott).....	3
FIG. 41. Plate with the most common style of ornamentation ($\times 6$).	
FIG. 42. Poorly preserved calyx with several attached arms ($\times 2.5$).	

PLATE 2

<i>Vistoia</i> ? <i>minuta</i> , new species.....	21
FIG. 1. Supposed cranidium ($\times 6$).	
FIG. 2. The holotype pygidium ($\times 6$).	
<i>Utia curio</i> Walcott.....	21
FIG. 3. Dorsal view of cranidium ($\times 2$).	
<i>Zacanthoides serratus</i> , new species.....	10
FIG. 4. Cranidium retaining left librigena ($\times 2$).	
FIG. 5. Pygidium, with exfoliated spines ($\times 2$).	
FIG. 6. Holotype with pygidium and thorax ($\times 2$).	

	PAGE
<i>Zacanthoides abbreviatus</i> , new species.....	10
FIGS. 7 ($\times 2$), 8. Small pygidia showing the stout axis.	
FIG. 9. Nearly complete holotype.	
<i>Zacanthoides holopygus</i> , new species.....	10
FIG. 10. Holotype.	
FIG. 11. Several individuals.	
FIG. 12. Pygidium ($\times 2$).	
<i>Elrathina offula</i> , new species.....	19
FIGS. 13 ($\times 2$), 14 ($\times 1.5$). Paratype and holotype cranidia.	
<i>Oryctocephalus walcotti</i> Resser.....	13
FIG. 15. Pygidium, thorax and doublure with attached hypostoma ($\times 1.5$).	
FIGS. 16 ($\times 1.5$), 18. Cranidia.	
FIG. 17. Pygidium ($\times 2$).	
<i>Poliella anteros</i> (Walcott).....	12
FIG. 19. Holotype.	
FIG. 20. Underside with hypostoma.	
<i>Poliella caranus</i> (Walcott).....	11
FIG. 21. Holotype ($\times 2$).	
<i>Oryctocare geikei</i> Walcott.....	14
FIG. 22. Holotype ($\times 5$).	
FIG. 23. Pygidium ($\times 2$).	
<i>Agnostus bonnerensis</i> Resser.....	8
FIG. 24. A good example ($\times 6$).	
FIGS. 25, 26. Separate shields ($\times 6$).	
<i>Agnostus brighamensis</i> , new species.....	8
FIG. 27. Holotype pygidium ($\times 6$).	
FIG. 28. Cranidium, <i>Pagetia</i> and <i>Lingulella</i> ($\times 6$).	
FIG. 29. Pygidium, <i>Oryctocephalus</i> and <i>Claspidella</i> ($\times 3$).	
Locality 20x.	
<i>Pagetia clytia</i> Walcott.....	8
FIG. 30. Several entire individuals ($\times 6$).	
FIG. 31. Cranidium ($\times 6$).	
FIG. 32. Pygidium ($\times 6$).	

PLATE 3

<i>Kootenia idahoensis</i> , new species.....	15
FIG. 1. Holotype.	
FIG. 2. Partially exfoliated pygidium.	
FIG. 3. Cranidium with occipital spine.	
<i>Kootenia spencei</i> , new species.....	15
FIG. 4. Holotype pygidium ($\times 1.5$).	
FIG. 5. Portion of pygidium showing pleural development ($\times 1.5$).	
<i>Kootenia matheysi</i> , new species.....	16
FIG. 6. Holotype pygidium.	
FIG. 7. Squeeze of an imperfect cranidium.	
Locality 20x.	

	PAGE
<i>Olenoides brighamensis</i> , new species.....	14
FIG. 8. Cranidium.	
FIG. 9. Squeeze of pygidium.	
Locality 20x.	
<i>Alokistocarella spencei</i> , new species.....	18
FIG. 10. Holotype cranidium.	
<i>Kootenia gracilis</i> , new species.....	16
FIG. 11. Squeeze of cranidium.	
FIG. 12. Holotype pygidium.	
Locality 20x.	
<i>Zacanthoides adjunctus</i> , new species.....	9
FIG. 13. Holotype.	
FIG. 14. Well-preserved pygidium.	
<i>Zacanthoides gradatus</i> , new species.....	9
FIG. 15. Well-preserved pygidium.	
FIG. 16. Cranidium with right librigenae.	
FIG. 17. Holotype.	
<i>Zacanthoides idahoensis</i> , new species.....	9
FIG. 18. Cranidium with occipital spine.	
FIGS. 19, 20. Nearly complete individuals.	

PLATE 4

<i>Olenoides wahsatchensis</i> (Hall and Whitfield).....	14
FIG. 1. Squeeze of cranidium.	
FIG. 2. Pygidium.	
Locality 20x.	
<i>Olenoides cransi</i> , new species.....	15
FIG. 3. Cranidium	
FIG. 4. Holotype.	
Locality 55e.	
<i>Alokistocare septum</i> , new species.....	17
FIG. 5. Individual showing brim well.	
FIG. 6. Small cranidium.	
FIG. 7. Holotype.	
<i>Alokistocare idahoense</i> , new species.....	16
FIG. 8. Librigenae ($\times 1.5$).	
FIG. 9. Holotype.	
<i>Alokistocare spencense</i> , new species.....	16
FIG. 10. Holotype.	
FIG. 11. Another individual showing pygidium and changed aspect due to broken brim.	
<i>Chancia ebdome</i> Walcott.....	17
FIG. 12. Cranidium.	
FIG. 13. Cranidium and displaced librigenae.	
FIG. 14. A well-preserved specimen.	

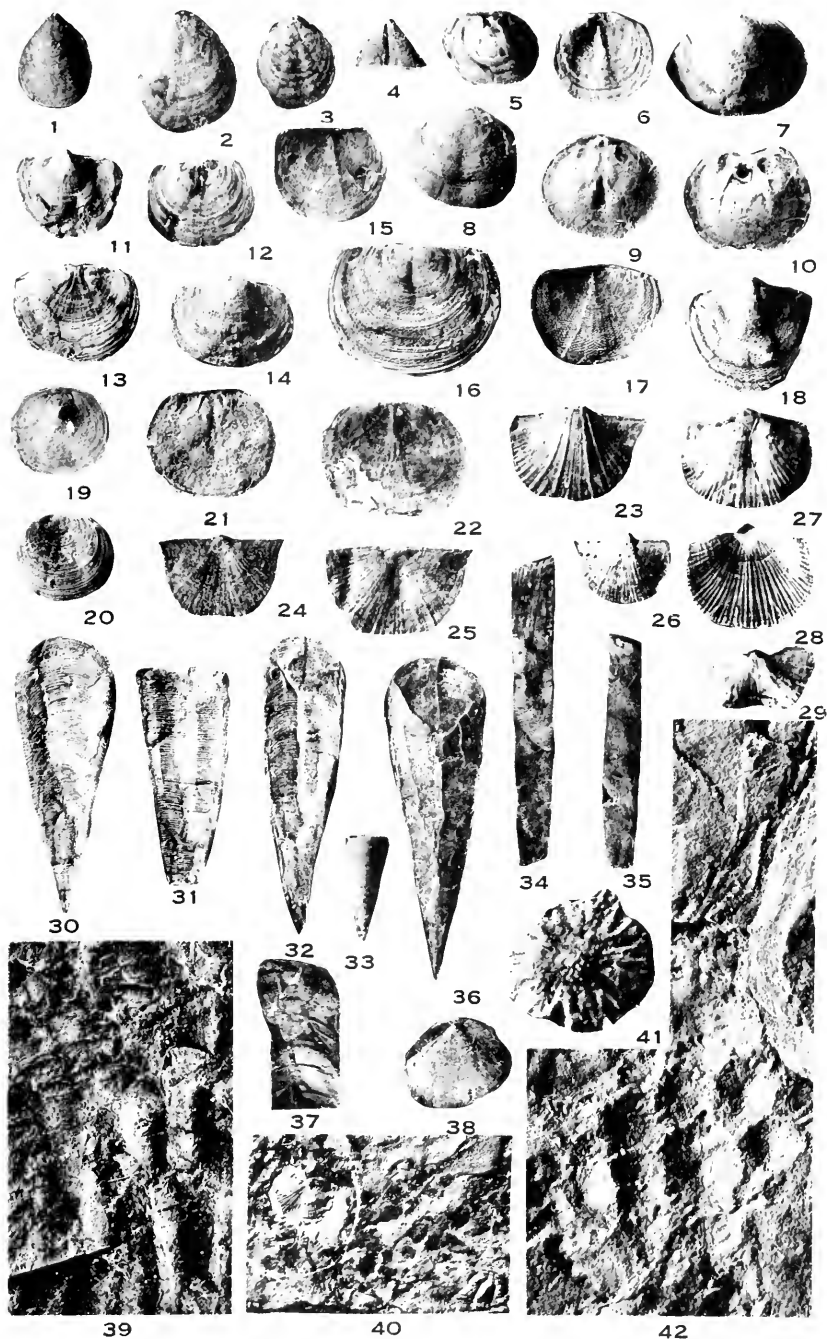
	PAGE
<i>Alokistocare laticaudum</i> , new species.....	17
Figs. 15, 16. Cranidia in calcareous shale.	
Locality 55e.	
FIG. 17. Incomplete individual.	
FIG. 18. Holotype.	
FIG. 19. Specimen lacking the librigenes.	
<i>Alokistocare punctatum</i> , new species.....	17
FIG. 20. Cranidium and portion of thorax.	
FIG. 21. Cranidium.	
Locality 55e.	

PLATE 5

<i>Glossopleura bion</i> (Walcott).....	12
FIG. 1. Cranidium and impression of pygidium.	
FIG. 2. Large pygidium.	
<i>Bathyriscus brighamensis</i> , new species.....	11
FIG. 3. Holotype.	
FIG. 4. Impression of pygidium.	
Locality 20x.	
<i>Clavaspidella anax</i> (Walcott).....	13
FIG. 5. Cranidium.	
FIG. 6. Lectotype.	
Locality 55e.	
<i>Staurololcus typicalis</i> , new species.....	24
FIG. 7. Exfoliated cranidium.	
FIG. 8. Holotype cranidium ($\times 2$).	
<i>Glossopleura similis</i> , new species.....	12
FIG. 9. Cranidium and librigenae with <i>Hyolithes cecrops</i> .	
FIG. 10. Pygidium.	
Locality 56 L.	
FIG. 11. Holotype pygidium.	
<i>Clavaspidella bilhus</i> (Walcott).....	13
FIG. 12. Lectotype pygidium.	
<i>Chancia angusta</i> , new species.....	18
FIG. 13. Paratype.	
FIG. 14. Holotype.	
<i>Bathyriscus atossa</i> Walcott.....	11
FIG. 15. Holotype.	
<i>Glossopleura utahensis</i> Resser.....	12
FIG. 16. Paratype pygidium.	
Locality 55e.	
<i>Glossopleura gigantea</i> , new species.....	13
FIG. 17. Holotype ($\times 5$).	
Locality 20x.	
<i>Chancia crax</i> Walcott.....	18
FIG. 18. Plesiotype cranidium.	
FIG. 19. Holotype.	

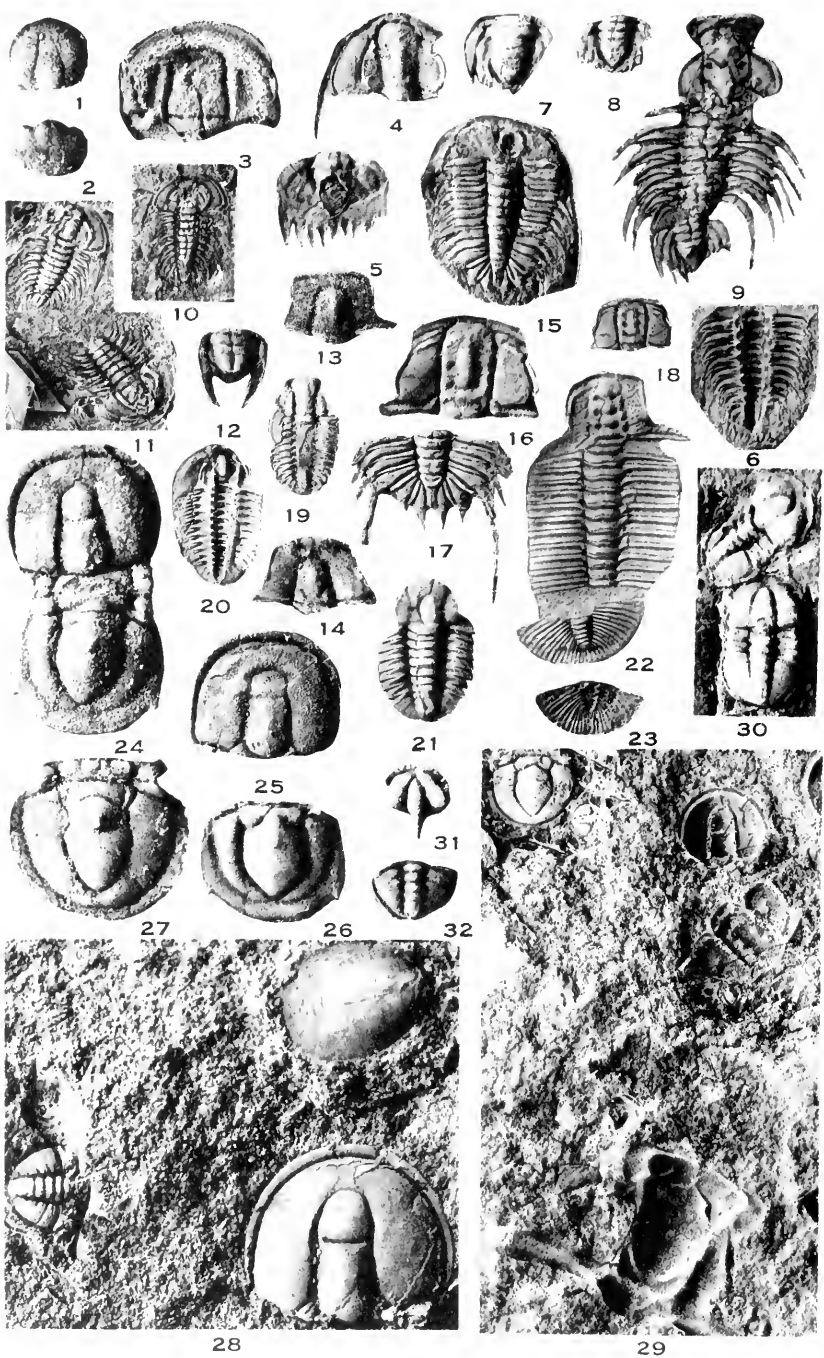
PLATE 6

	PAGE
<i>Bythichcilus typicum</i> , new species.....	22
FIG. 1. Complete individual and cranium ($\times 1.5$).	
FIG. 2. Individual lacking librigenes ($\times 2.5$).	
FIG. 3. Holotype ($\times 2$).	
FIG. 4. Small example ($\times 3$).	
<i>Clappaspis spencei</i> , new species.....	20
FIG. 5. Exfoliated cranium.	
FIG. 6. Partially exfoliated holotype ($\times 2$).	
<i>Clappaspis lanata</i> , new species.....	20
FIG. 7. Holotype ($\times 1.5$).	
<i>Bythichcilus alveatum</i> , new species.....	22
FIG. 8. Exfoliated cranidia ($\times 2.5$).	
FIG. 9. Exfoliated conventionally lighted cranium ($\times 2$).	
FIG. 10. Holotype ($\times 2.5$).	
<i>Clappaspis coriacea</i> , new species.....	20
FIG. 11. Cranium.	
FIG. 12. Holotype cranium ($\times 2$).	
<i>Clappaspis dotis</i> , new species.....	21
FIG. 13. Cranium, with <i>Spencia plena</i> ($\times 2$).	
FIG. 14. Holotype ($\times 2$).	
<i>Elrathia spencei</i> , new species.....	18
FIG. 15. Holotype ($\times 2$).	
FIG. 16. Smaller individual retaining librigenes ($\times 2$).	
FIG. 17. Exfoliated specimen ($\times 2$).	
<i>Elrathia rara</i> , new species.....	19
FIG. 18. Holotype ($\times 2$).	
<i>Spencia plena</i> , new species.....	23
FIG. 19. Partially exfoliated holotype cranium ($\times 3$).	
FIG. 20. Small cranium ($\times 3$).	
FIG. 21. Cranidia with <i>Bythichcilus alveatum</i> ($\times 2$).	
<i>Spencia typicalis</i> , new species.....	23
FIG. 22. Cranium showing granules ($\times 1.5$).	
FIG. 23. Small cranium ($\times 1.5$).	
FIG. 24. Holotype ($\times 2$).	
FIG. 25. Cranium ($\times 1.5$).	
<i>Clappaspis idahoensis</i> , new species.....	20
FIG. 26. Holotype.	
FIG. 27. Two smaller individuals.	
<i>Ehmaniella quadrans</i> (Hall and Whitfield).....	19
FIG. 28. Original type of cranium ($\times 2.5$).	
FIG. 29. A less distorted cranium ($\times 3$).	
FIG. 30. Associated librigena ($\times 2.5$).	
FIG. 31. Pygidium ($\times 3$).	
Locality 20x.	
FIG. 32. Limestone nodule with cranidia and fragments of pygidia.	
Locality 55e.	

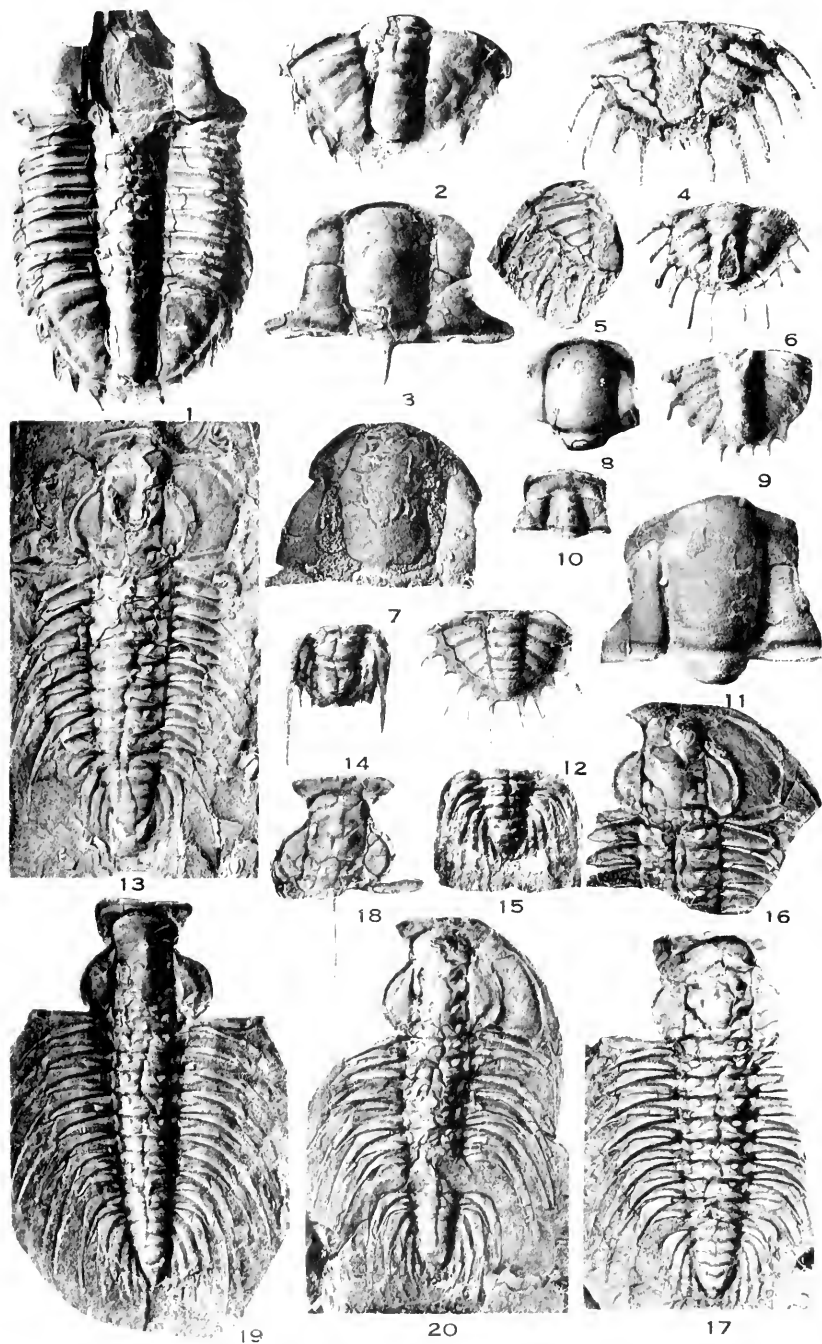


BRACHIOPODS, HYOLITHES, AND OTHER FOSSILS

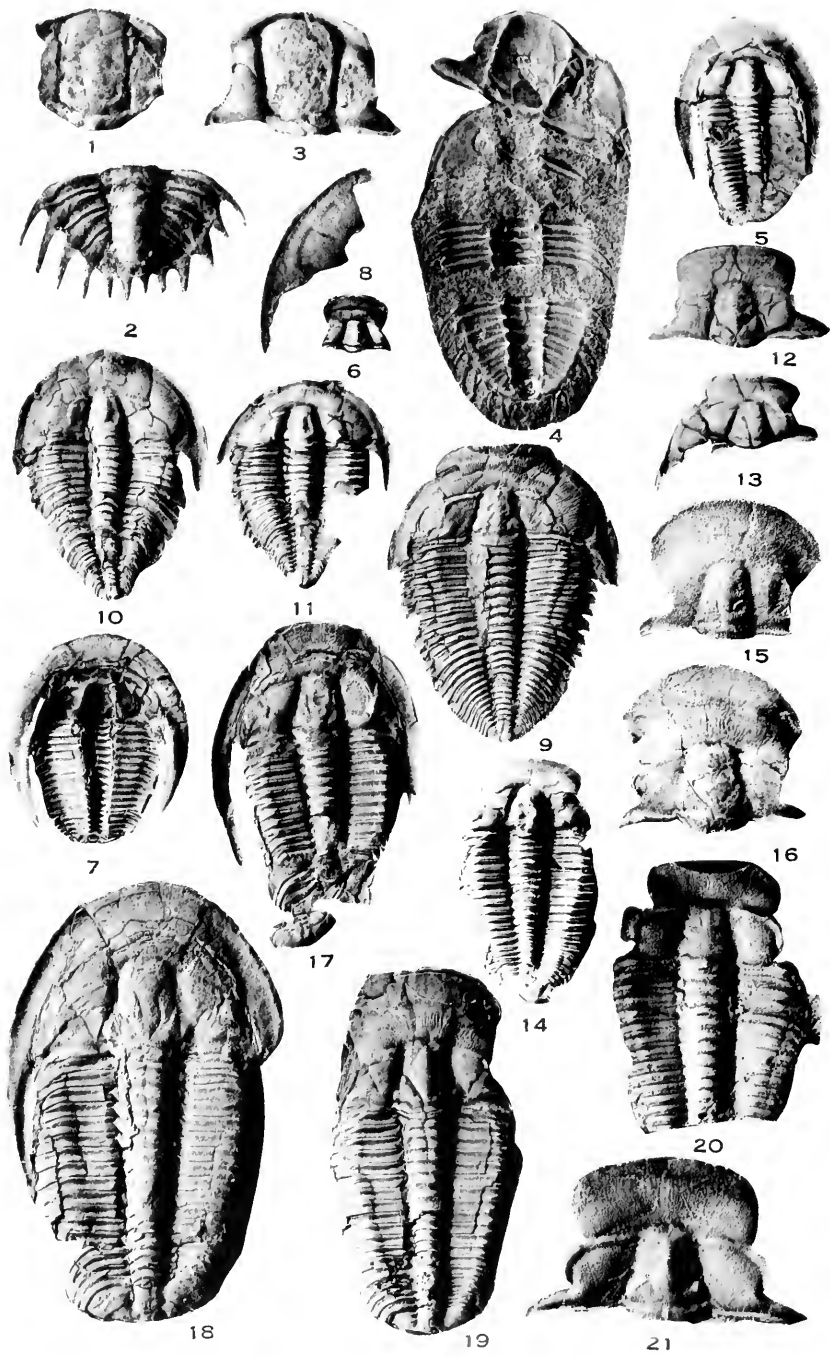
(See explanation of plates at end of text.)



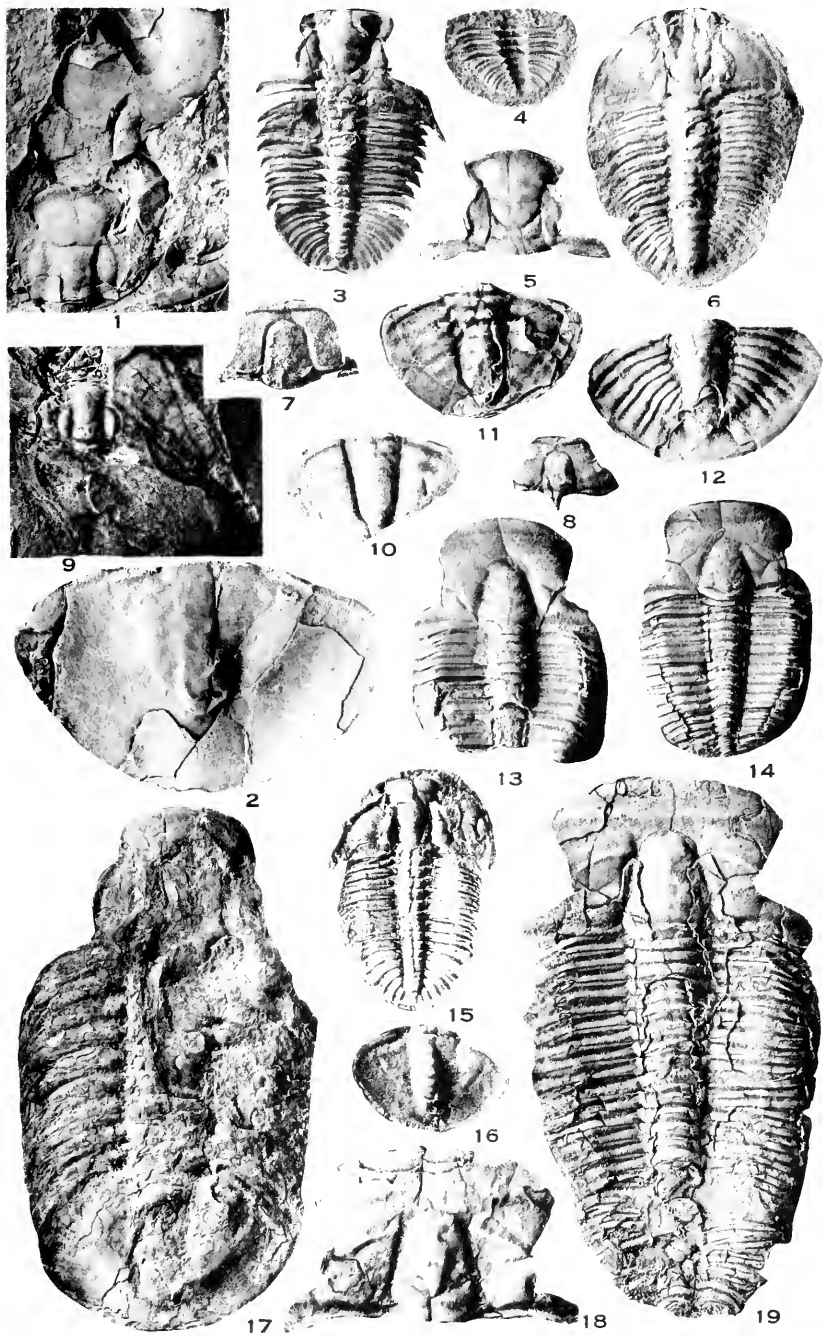
AGNOSTIDA AND TRILOBITES
(See explanation of plates at end of text.)



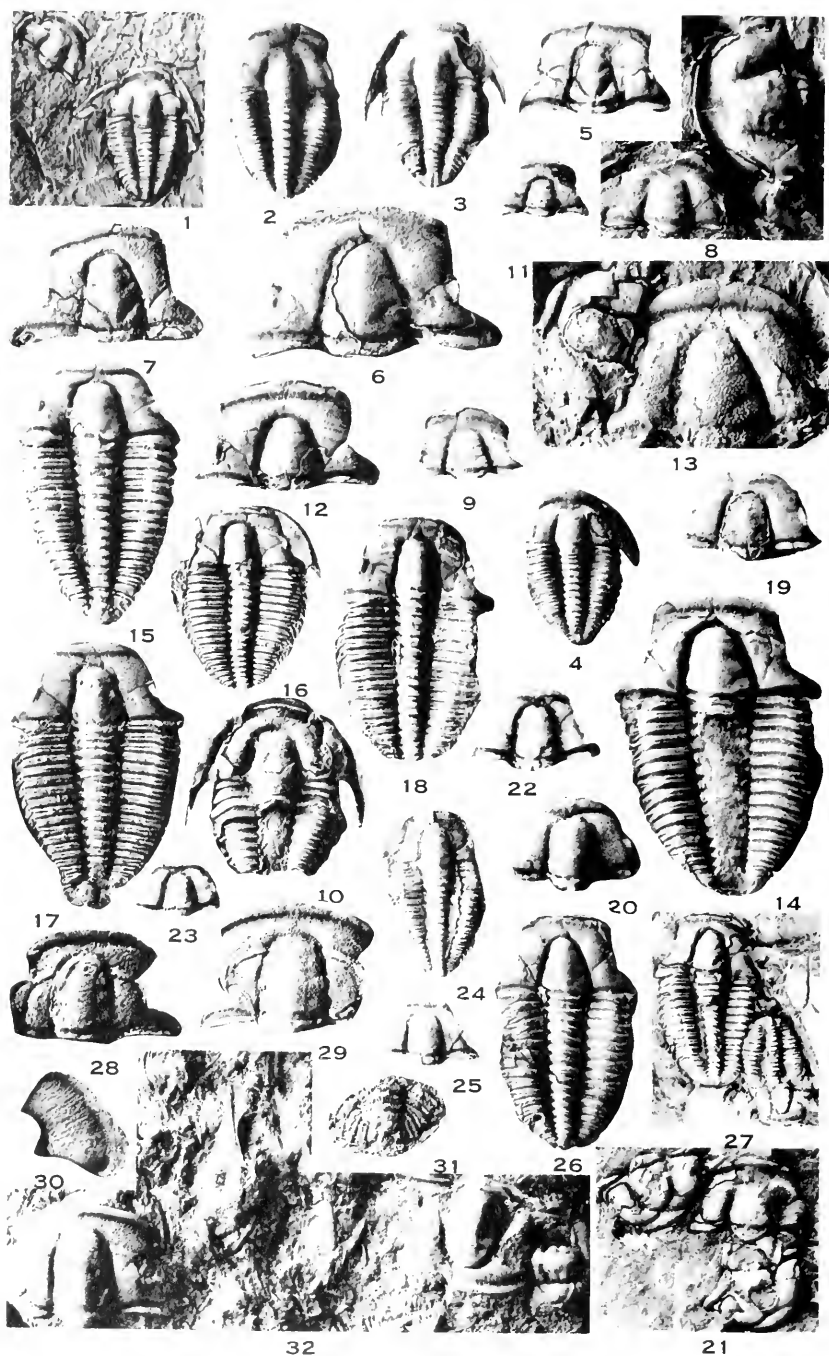
KOOTENIA, OLENOIDES, AND ZACANTHOIDES
(See explanation of plates at end of text.)



OLENOIDES, ALOKISTOCARE, AND CHANCIA
(See explanation of plates at end of text.)



SPENCE SHALE TRILOBITES
(See explanation of plates at end of text.)



SPENCE SHALE TRILOBITES

(See explanation of plates at end of text.)











GEORGE A.
SIMONDS
& CO.
930 H ST., N.W.
WASHINGTON, D.C.

SMITHSONIAN INSTITUTION LIBRARIES



3 9088 01421 4852